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A NEW BASELINE FOR *DIADEMA ANTILLARUM*, *ECHINOMETRA VIRIDIS*, *E. LUCUNTER*, AND *EUCIDARIS TRIBULOIDES* POPULATIONS WITHIN THE CAYOS COCHINOS MPA, HONDURAS

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ABSTRACT: We investigated the density of 4 urchin species from 5 shallow reefs in the Cayos Cochinos Marine Protected Area in Honduras. Individual species density varied among reefs with total urchin density ranging from 3.2–7.9 individuals/m². *Echinometra viridis* (Agassiz, 1863) was the numerically dominant species (2.29/m²) followed by *E. lucunter* (Linnaeus, 1758) (1.76/m²) with *Eucidaris tribuloides* (Lamarck 1816) representing the fewest individuals (0.42/m²). Our results indicated that density of *Diadema antillarum* (Philippi, 1845) differed significantly among reefs (0.4–1.3/m², mean = 0.63/m²), but are three times greater than data collected 12 years after the mass mortality event of the 1980's. Size frequency analysis of *D. antillarum* indicated that test diameter also differed significantly among reef sites while correlation analysis showed that *D. antillarum* density was negatively related to both coral and algal cover. *Echinometra viridis* density, however, was positively related to coral cover ($p < 0.05$). When all urchins were combined, they showed a negative correlation with algal cover and a positive correlation with coral cover indicating a potential top–down effect within the reefs. While urchin densities remain relatively low compared to other sites in the Caribbean, the *D. antillarum* population appears to be recovering in this Honduran MPA. If overall grazer abundance continues to increase then they may limit macroalgae on reefs, thereby encouraging coral settlement.

KEY WORDS: sea urchin, coral reef, Caribbean, top–down

INTRODUCTION

Urchins are important herbivores in tropical reef systems. The devastating mass mortality of *Diadema antillarum* in the Caribbean during the 1980's (Lessios et al. 1984b) contributed to substantial shifts in reef community structure (Bruno et al. 2009, Mumby 2009). Substantial declines in coral cover have been observed throughout the region (Gardner et al. 2003), surmised to be the result of epidemic disease presence in corals, elevated algal growth due to the loss of herbivores, and natural and anthropogenic disturbances; thus leading to the potential of community phase shifts and loss of resilience (Norström et al. 2009, Hughes et al. 2010). While some areas have seen recovery in *D. antillarum* populations (Edmunds and Carpenter 2001, Ruiz—Ramos et al. 2011), others are still plagued with substantially reduced population sizes and high algal cover (Harborne et al. 2009). Although the loss of *D. antillarum* is certainly not the only cause of the decline in coral cover, the system shift discussed by Hughes (1994) and Bruno et al. (2009) demonstrates the necessity of understanding population dynamics and inventory of urchin populations throughout the Caribbean as part of a comprehensive approach for reef management. If recovery of *D. antillarum* populations leads to reduced algal cover, then perhaps some coral recovery is possible by opening up settlement sites (Carpenter and Edmunds 2006, Mumby et al.

2007a). However, *D. antillarum* is not the only reef echinoid. Lessios et al. (1984a) demonstrated that after the mass mortality, *Echinometra viridis* and *E. lucunter* showed significant increases in their density on Caribbean reef flats, potentially filling the grazing niche voided by the die–off, and currently they are a numerically dominant echinoid grazer on some reefs (Brown—Saracino et al. 2007).

One interesting observation regarding the recovery and distribution of *D. antillarum* after the mass mortality event relates to system protection. Harborne et al. (2009) reported that in regions that were open to fishing, *D. antillarum* were present, while in the preserve, they were absent. They surmised that it was the increase in larger predatory fish present in the protected area that led to predation pressure on *D. antillarum* and may have limited their recovery. Similarly, Brown—Saracino et al. (2007) reported their lowest urchin density in the Marine Protected Areas (MPA). However, Blanco et al. (2010) observed the opposite trend with significantly greater densities of *D. antillarum* within the marine reserve compared to non—reserve sites in Cuban reefs. As such, in MPAs the recovery of coral reefs may be impeded by low urchin densities unless alternate herbivores are present to eliminate substantial algal growth (McClanahan et al. 1996, Mumby et al. 2006, 2007a, Mumby and Harborne 2010).

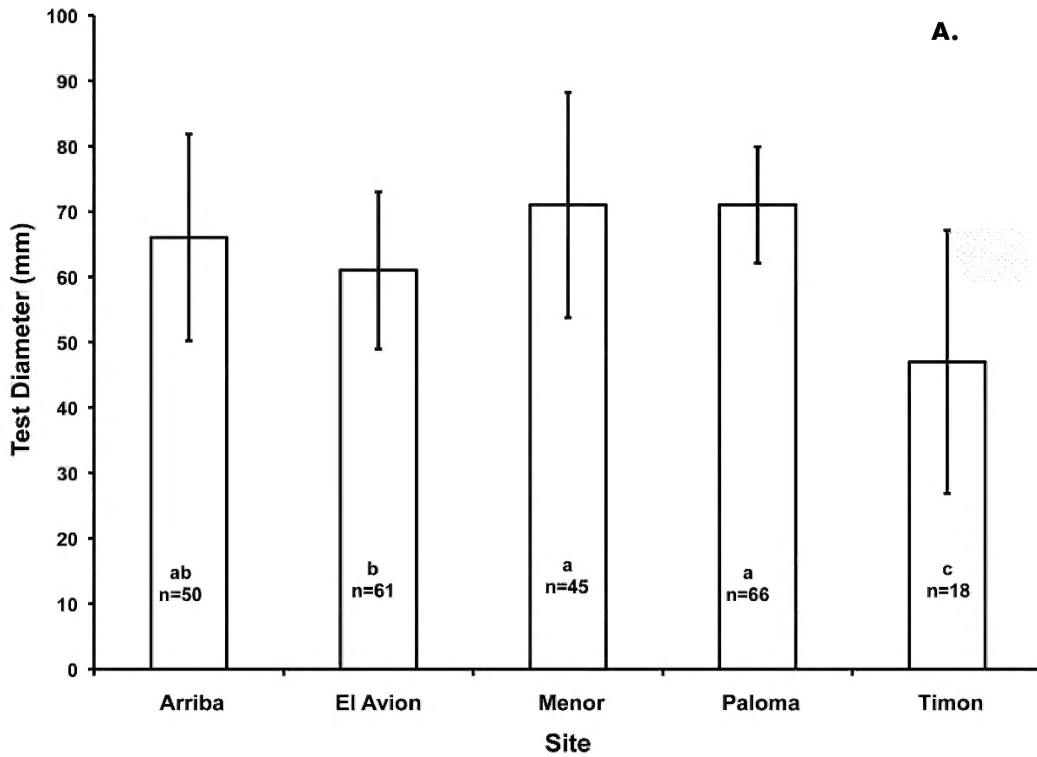
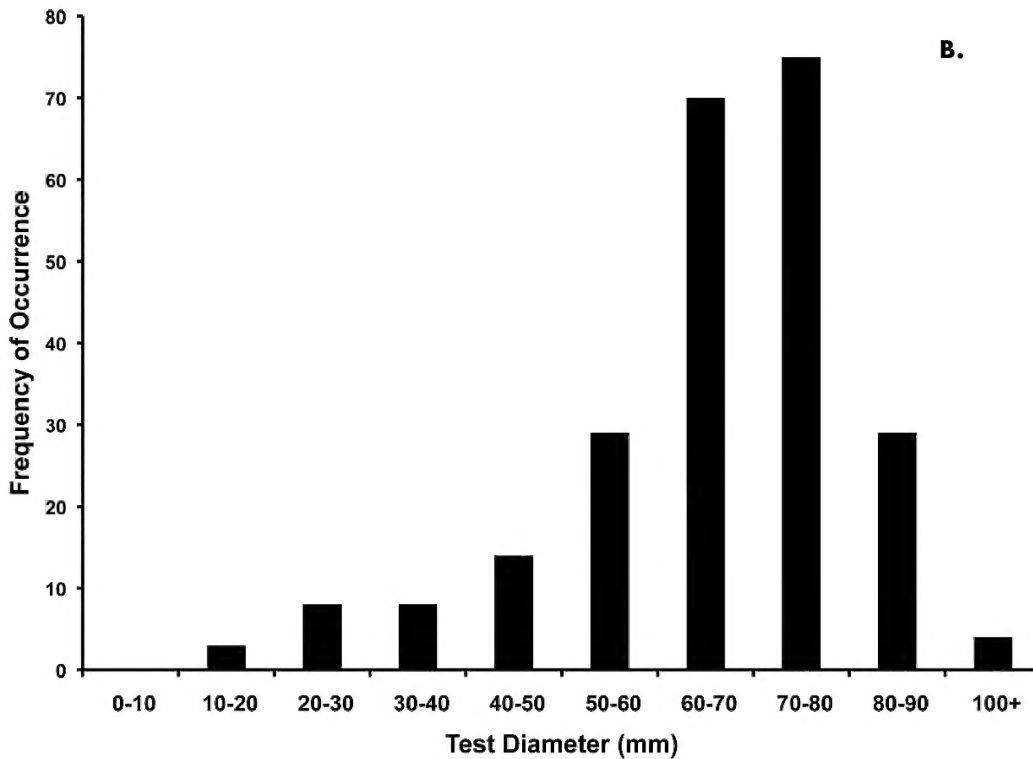


Figure 1. Urchin population demographics among the reefs sampled. **A.** Mean test diameter (\pm SD) among reef sites. Significant differences designated by unique letters. **B.** Combined *Diadema antillarum* population size frequency distribution. $n = 240$.



In Honduras, the Cayos Cochinos archipelago was designated a Marine National Monument in 1993 by the Honduran government. The aim of the designation is conservation and management of the regions' natural resources as well as economic stability. In particular, tight fishing regulations were enacted to protect and enhance fish populations. The islands comprise the very southern tip of the Mesoamerican

Barrier Reef System and were recognized as an important site of biodiversity in the area by the establishment of the MPA and designation as a Marine National Monument. The MPA has a no fishing core zone and a buffer zone with differing levels of fishing effort for select species at certain times of the year. The reefs surveyed in this study were all contained within the core zone. One emerging area of research in this

TABLE 1. Reef survey results among sites. Values represent the mean urchin density ($\#/m^2 \pm SD$) or the mean spatial coverage (% cover $\pm SD$). Differing letters next to means indicate significant differences among sites.

Site	<i>Echinometra viridis</i>	<i>Echinometra lucunter</i>	<i>Diadema antillarum</i>	<i>Eucidaris tribuloides</i>	Coral Cover	Algal Cover
Arriba	2.27 \pm 1.28 ^{ab}	1.71 \pm 1.59	0.06 \pm 0.09 ^b	0.13 \pm 0.07 ^b	29.0 \pm 15.5	30.1 \pm 9.3
Menor	0.97 \pm 0.55 ^b	2.53 \pm 1.43	0.18 \pm 0.19 ^b	0.37 \pm 0.12 ^b	18.6 \pm 8.1	39.9 \pm 9.1
Paloma	0.97 \pm 1.20 ^b	0.97 \pm 0.74	1.01 \pm 0.71 ^{ab}	0.29 \pm 0.15 ^b	10.8 \pm 5.0	33.5 \pm 23.1
El Evion	4.55 \pm 3.43 ^a	1.02 \pm 0.72	1.38 \pm 1.08 ^a	0.96 \pm 0.57 ^a	19.0 \pm 9.0	40.8 \pm 14.2
Timon	2.68 \pm 2.40 ^{ab}	2.59 \pm 2.85	0.54 \pm 0.53 ^{ab}	0.38 \pm 0.23 ^b	25.1 \pm 16.3	25.2 \pm 5.6
p-value	0.03	0.28	0.006	0.0007	0.11	0.26

MPA is urchin dynamics and the recovery of *D. antillarum* to this reef system. Lessios (1998) conducted the only estimate of urchin populations within the MPA by sampling a variety of habitats. In this study, we focus on reporting a new baseline for echinoid populations on shallow reefs.

MATERIALS AND METHODS

Research was conducted during the summer of 2009 on five reefs associated with the Cayos Cochinos MPA in Honduras: Cayos Arriba (15°57.5'N, 86°27.9'W), El Avion (15°57.2'N, 86°29.0'W), Menor (15°57.4'N, 86°30.4'W), Paloma (15°56.4'N, 86°30.0'W) and Timon (15°55.8'N, 86°32.6'W). Cayos Timon and Paloma represent shallow reef sites that were examined previously by Lessios (1998, his sites 1 and 5, respectively) for echinoid abundance. Snorkelers surveyed reef flats (1–3 m) for urchins, coral cover and algal cover using haphazardly selected 15 x 2 m transects laid out on the reefs (n = 6 surveys/reef site) during daylight hours. Transects were a minimum of 15 m apart. Abundance of the four most common urchins (*D. antillarum*, *E. lucunter*, *E. viridis*, and *Eucidaris tribuloides*) was counted along each transect and standardized to number/m². Prior to analysis, data were square root transformed to eliminate heteroscedacity and then compared among reefs using a one-way ANOVA. Coral and algal coverage were estimated visually by pooling five 1m² gridded quadrat samples (10 cm x 10 cm sub-grids) collected along the length of the transect. Specific sampling locations were selected *a priori* at distance intervals of 0–1 m, 3–4 m, 6–7 m, 9–10 m and 12–13 m along the transect. Initial samples were collected randomly (right or left), then each subsequent sample was collected on the alternate side. We recognize the limitations of visual estimates, but all samples were collected in the same manner and provide a context of spatial coverage. While species were identified to lowest reasonable taxa in the field, individual coral and algal taxa varied highly among reefs and transects and subsequently, these data were pooled into broad categories of coral and algal spatial coverage. Correlation analyses were then carried out on urchin species density, total urchin abundance, coral cover, and algal cover to assess potential relationships. Additionally, *D. antillarum* test diameter was measured in

the field using 40 cm stainless steel tree calipers on as many urchins that were present and measurable during a 50 min sampling period (n = 240) for each of the 5 reefs. Measurements of *D. antillarum* reflect a sequential survey measuring any individual encountered during the sampling period. We recognize that the smallest *D. antillarum* are highly cryptic, so care was taken to investigate potential refugia for small individuals. However, it is possible that the smallest individuals were not measured due to their cryptic nature. Urchin test diameter was then compared among reefs using a one-way ANOVA and discriminated using REGWQ pairwise comparisons (SAS®).

RESULTS

Densities of *D. antillarum* ($F_{4,25} = 4.62$, $p < 0.007$), *E. viridis* ($F_{4,25} = 3.13$, $p < 0.03$) and *E. tribuloides* ($F_{4,25} = 6.95$, $p < 0.001$) varied significantly among reefs investigated, while those of *E. lucunter* did not (Table 1). Additionally, our results showed that coral cover was relatively low and macroalgal cover high, but neither differed among reefs (Table 1). Our correlation analyses indicated a significant negative relationship between *D. antillarum* density and coral cover (Pearson $r = -0.43$, $p < 0.02$), but positive correlation between *E. viridis* and coral cover ($r = 0.36$, $p < 0.05$). No other factors showed significant relationships, but total urchin abundance was negatively correlated with algal cover ($r = -0.32$, $p > 0.08$) and positively correlated with coral cover ($r = 0.13$, $p > 0.4$). While *D. antillarum* density was low at all sites, test diameter was large and differed significantly among reefs ($F_{4,235} = 13.06$, $p < 0.0001$), with urchins from Menor and Paloma being larger than urchins collected at the other three sites (Figure 1A). The overall size frequency distribution demonstrates that for the Cayos Cochinos region, one large population peak occurs in the 60–80 mm size range, but the presence of small individuals (12 mm test diameter) indicates that recruitment is occurring (Figure 1B).

DISCUSSION

The mass die-off of *D. antillarum* left many Caribbean coral reef systems devoid of a primary herbivore (Lessios 1988), but in some cases reef communities showed increases of other echinoids possibly due to the abatement of competi-

tion (Lessios et al. 1984a). Regardless, the subsequent shift from a coral dominated system to one that reflects high algal abundance occurred in many regions of the Caribbean (Carpenter 1990). In 1995, Lessios (1998) assessed the reefs within the Cayos Cochinos MPA for the presence of echinoids. Based on his results, reef echinoid density was about $4.7/\text{m}^2$ and was dominated by *E. lucunter* ($3.8/\text{m}^2$) with lesser amounts attributed to *E. tribuloides* and *E. viridis* (0.47 and $0.24/\text{m}^2$, respectively), and *D. antillarum* ($0.19/\text{m}^2$). Our results showed similar densities of *E. tribuloides*, but 40% fewer *E. lucunter*. The biggest differences observed relate to a tripling of *D. antillarum* density and an order of magnitude increase in *E. viridis*.

Our results indicate that urchin populations are potentially recovering, but *D. antillarum* density is still far below the densities of other Caribbean reefs (Carpenter and Edmunds 2006) and total urchin density is far below those observed elsewhere (Brown–Saracino et al. 2007). For *D. antillarum*, Carpenter (1990) describes densities for St. Croix, USVI ranging from 5.8–13 individuals/ m^2 prior to the mass mortality, but recovery there has seen densities range as high as $5/\text{m}^2$ and this is similar to densities observed on Jamaican reefs (Edmunds and Carpenter 2001). This increase in density, with subsequent reduction in macroalgal cover, has allowed elevated coral recruitment (Carpenter and Edmunds 2006). While the loss of urchins is surmised to have been a proximal mechanism used to describe the phase shift between coral and macroalgal dominated communities, recent assessments demonstrate the complexity of coral reef structuring mechanisms (Bruno et al. 2009, Mumby 2009, Hughes et al. 2010). One challenge that we face is the limited historical data regarding the structure of this coral reef system. Our data suggest that coral cover is low and macroalgal cover relatively high (Table 1), but greater efforts in assessing all critical parts of the reef community are needed before generalizations are possible for Cayos Cochinos. Correlation analyses showed a positive correlation between *E. viridis* and coral cover, but a negative one for *D. antillarum*. While this may appear contrary to the concept that *D. antillarum* abun-

dance has a positive impact on coral recruitment, the lack of response may merely be an artifact of a system in recovery and further research should clarify this issue. However, total urchin abundance was negatively correlated with algal cover and positively with coral cover, so the combined grazing pressure by echinoids may be setting the stage for greater recovery. In fact, our density of *E. tribuloides* is similar to that reported in the Florida Keys by Chiappone et al. (2002), but density of *E. viridis* was 4–10x higher than theirs, and an order of magnitude greater for *D. antillarum*. Consequently, the lack of recovery seen in many reefs in the Florida Keys may relate to substantially lower combined grazer abundance, and not just the lack of *D. antillarum*, coupled with natural and anthropogenic disturbance (Hughes 1994, Mumby et al. 2007b).

While *D. antillarum* density was low at all sites, the collection of small individuals suggests that recruits are coming into the system. As such, recovery of *D. antillarum* on these reefs is possible. However, with no pre-mortality population density and size data, it may be impossible to infer whether *D. antillarum* populations have ‘recovered’ (*sensu* Lessios 2005). Additionally, the restrictions on fishing may change trophic structure of these reefs leading to changes in predation pressure on juvenile and new recruits, which may differentially impact the density and size distribution of *D. antillarum* (*sensu* Clemente et al. 2009). However, if this site is recruitment limited due to regional populations (*sensu* Miller et al. 2009), then population increases may not occur above some limited threshold until large scale recovery of *D. antillarum* occurs in the Caribbean. Carpenter and Edmunds (2006) demonstrate that when *D. antillarum* populations increase, coral recruitment can increase as well. Consequently, the regional recovery of *D. antillarum* may signal a starting recovery for Caribbean reefs (Mumby 2009, Mumby and Harborne 2010). As such, continued assessment of urchins, and specifically *D. antillarum*, coupled with algal and coral coverage in the shallow reefs is necessary to establish baseline conditions upon which future management and reef assessments can be made.

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A Western Range Extension for *Caprella scaura* (Amphipoda: Caprellidae) in the Aransas Bay Ecosystem, Texas

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A WESTERN RANGE EXTENSION FOR *CAPRELLA SCAURA* (AMPHIPODA: CAPRELLIDAE) IN THE ARANSAS BAY ECOSYSTEM, TEXAS

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ABSTRACT: During March 2009, the skeleton shrimp *Caprella scaura* and *Paracaprella tenuis* (Amphipoda: Caprellidae) were collected from several locations throughout the Aransas Bay, Texas ecosystem from Texas Parks and Wildlife fishery-independent trawl and oyster dredge samples. This is a western range expansion for *C. scaura*; *P. tenuis* has been reported from this area before. Both species were exclusively associated with a bryozoan, *Bugula neritina*. Densities of both species ranged between 0.1–3.4 individuals per gram of attached bryozoans. A reproductive population is likely established since several sizes, including adult males and gravid females, were observed. No caprellids were observed after early April, which coincided with a reduction in bryozoan occurrence in our routine monthly samples. These collections represent the first documented occurrence of *C. scaura* west of Florida.

KEY WORDS: Caprellidae, *Caprella scaura*, *Paracaprella tenuis*, skeleton shrimp, amphipods

INTRODUCTION

Several species of amphipod from the family Caprellidae are known to occur in the Gulf of Mexico (GOM): *Caprella andreae*, *C. equilibra*, *C. penantis*, *C. scaura*, *Deutella incerta*, *Hemiaegina minuta*, *Paracaprella pusilla*, *P. tenuis*, and *Phtisica marina* (Foster et al. 2004b). Only 5 of these species have been recorded in Texas coastal waters near Port Aransas: *H. minuta*, *D. incerta*, *P. pusilla*, *P. tenuis*, and *C. equilibra* (Foster et al. 2004b). *Caprella scaura* was first documented by Templeton (1836) in the Indian Ocean near Mauritius. The species is widely distributed and has been documented in all oceans but the Arctic (Foster et al. 2004a). However, the first collections from coastal waters of the United States were recently documented in Charleston Harbor, South Carolina and St. Andrew Bay, Florida (Foster et al. 2004a). The only other western Atlantic collections occurred in the Virgin Islands, Puerto Rico and Brazil, where they have been associated with benthic substrates (McCain 1968).

Most caprellids are suspension feeders that cling to benthic substrates (i.e. macroalgae, seagrasses, bryozoans, and hydroids); however, some species have been collected from mobile substrates (i.e., *Sargassum* and sea turtles) (Keith 1969; Caine 1978; Takeuchi and Hirano 1995; Díaz et al. 2005). Several such substrates exist in Aransas and Mesquite Bays, Texas. Here, we present results indicating a western range extension for *C. scaura* in Aransas and Mesquite Bays, Texas, with density and identification information.

MATERIALS AND METHODS

Collection Area

Aransas Bay is a major bay along the central Texas coast, located between San Antonio Bay and Corpus Christi Bay. The Aransas Bay ecosystem consists of 5 secondary bays (Copano Bay, Redfish Bay, St. Charles Bay, Carlos Bay and

Mesquite Bay) and 2 tertiary bays (Mission Bay and Port Bay) that total 45,311 ha. Aransas Bay is connected to the GOM with an inlet at Port Aransas. The Guadalupe, San Antonio, Aransas and Mission Rivers contribute nearly all of the fresh water inflow to the bay. Habitats found in the bay system include: unconsolidated sediments, eastern oyster reefs, submerged seagrass meadows, emergent marsh, and mangrove stands. Macroalgae and seagrasses are well established there year round, although seagrass senescence typically begins mid–October, which results in a reduction of available above–ground substrates in these bays. *Sargassum*, floating brown algae, is present mostly during summer months when it accumulates on beach shorelines and enters the bays through Gulf passes (Texas Parks and Wildlife Department (TPWD) unpublished data). Bryozoans closely associated with hard substrates such as eastern oyster reefs have been collected year round, but at greater densities during spring months. Many species of sea turtles occur in the area; however, no turtles were captured in sample gear during this observation period. Most collections of caprellids were sampled in Aransas Bay proper with the exception of one collection in Mesquite Bay (Figure 1).

Sampling methodology

Bay trawls and oyster dredges were used to collect caprellid species during this study. The Coastal Fisheries Division of TPWD bay trawl and sampling procedures and gear specifications have been standardized since 1982. Bay trawls are 6.1 m long benthic otter trawls, with mesh that measures 38 mm stretched and is constructed of multifilament nylon. Trawl doors are 1.2 m long x 0.5 m wide and are constructed of 1.3 cm thick plywood with angle iron framework and iron runners. Trawls are pulled from the stern of research vessels at 4.8 k/h, completing one large circle in 10 minutes while

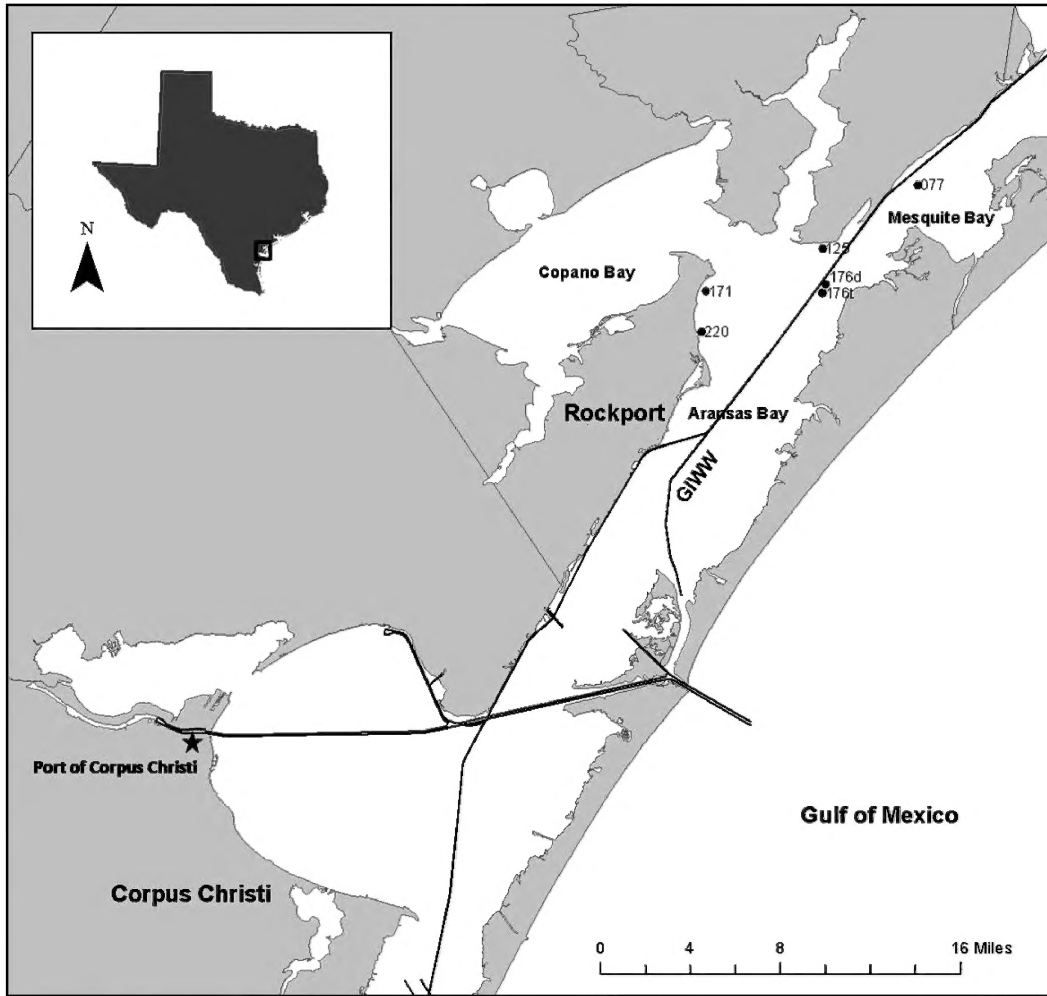


Figure 1. – Collection area within the Aransas Bay Ecosystem, Texas, indicating proximity to the Port of Corpus Christi, Gulf Intracoastal Water Way (GIWW, black lines), and sample site locations.

staying within one minute latitude by one minute longitude grids (Martinez–Adrande and Fisher 2010).

Similarly, TPWD oyster dredge sampling procedures and gear specifications have been standardized since 1985. Oyster dredges measure 0.5 m wide and 1.0 m tall. The dredge framework is constructed of 13 mm cold rolled steel round bar. The mesh bag is 356 mm deep and constructed of 76

mm stretched braided nylon solid core webbing. Dredges are towed from the stern of research vessels at 4.8 k/h for 30 sec, following the contour of the selected reef habitat (Martinez–Adrande and Fisher 2010).

Physicochemical, geographical, and sample–specific parameters were collected at each site. Water depth (m) was recorded using onboard sonar. Salinity, dissolved oxygen

TABLE 1. Aransas Bay sample sites, date, location, and gear type used in collecting samples of *Bugula neritina* containing caprellids, with number of individuals and density of *Caprella scaura* and *Paracaprella tenuis* collected for each site and gear type.

Location				Species Present		Density	
Site	Date	Latitude	Longitude	Gear	<i>Caprella scaura</i>	<i>Paracaprella tenuis</i>	n
220	3/9/2009	28.06639°N	97.0308°W	oyster dredge	X		75
125		28.11889°N	96.9417°W	bay trawl	X		3.43
176d ^b		28.09583°N	96.9397°W	oyster dredge	X		1.16
176c ^c		28.09028°N	96.9425°W	bay trawl	X		0.16
077		28.15889°N	96.8714°W	bay trawl	X	X	0.09
171 ^d	4/7/2009	28.09278°N	97.0272°W	oyster dredge	X		1.27

^a – no weight collected from *Bugula neritina*

^b – dredge sample at site 176

^c – trawl sample at site 176

^d – collection was subsampled due to large amount of bryozoans

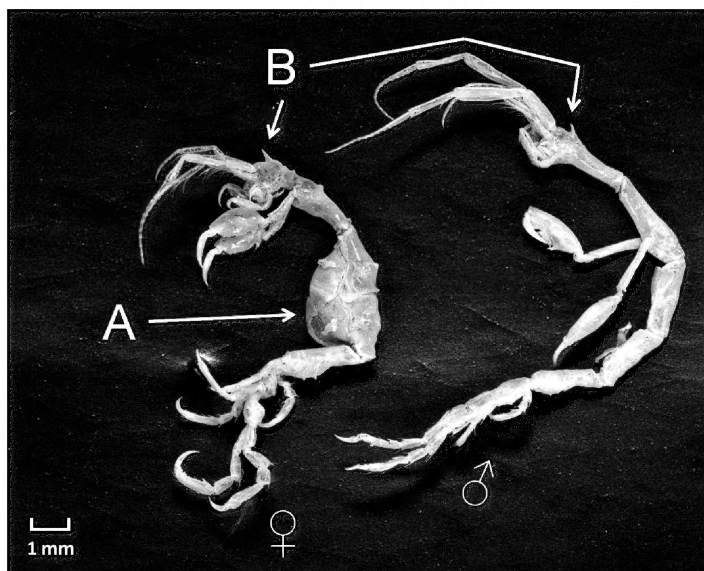


Figure 2. – Dissecting scope photo of individuals taken from Aransas Bay study samples include a female (♀) and male (♂) *Caprella scaura* illustrating brood pouch of female (A), and presence of spine on head (B).

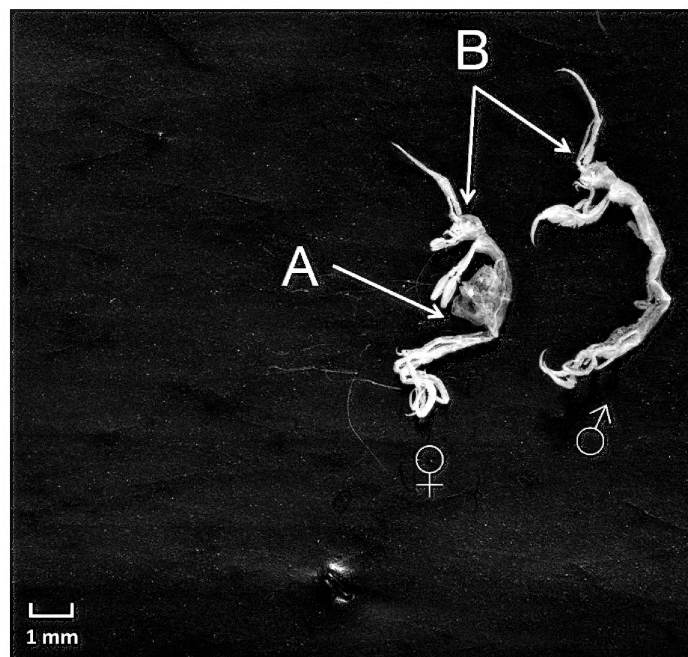


Figure 3. – Dissecting scope photo of individuals taken from Aransas Bay study samples include a female (♀) and male (♂) *Paracaprella tenuis* illustrating brood pouch of female (A) and absence of spine on head (B).

(mg/L), and water temperature (°C) were determined using a handheld multimeter within 15 cm of the substrate. Site code, date, coordinates (latitude and longitude), and collection gear were recorded.

Species, number collected, and calculated densities were also recorded, but because caprellids are difficult to sort in the field due to their clinging behavior, all substrates observed to have specimens were stored in labeled bags and placed on ice in the field. Sample collections were transported to the TPWD Rockport Marine Laboratory, Rockport, Texas. Once in the laboratory, samples were placed in sorting trays and all caprellids were identified and counted. Foster et al. (2004b) was used to key species and identifications were cross-referenced with McCain (1968) and Krapp et al. (2006). After identification, voucher specimens were sent to specialists at the University of Southern Mississippi, Gulf Coast Research Laboratory, Ocean Springs, MS for confirmation. Densities of attached caprellids were calculated as the number of individuals per wet weight of attached substrate (g). Sex was determined by the presence of brood pouches on gravid females and the morphology of the second gnathopods and anterior pereonites on males. Gender of juveniles was indistinguishable.

Subsampling was conducted for a single sample (site # 171; Table 1) which contained a large quantity of bryozoans and caprellids. The methods employed for the subsample consisted of weighing a portion of bryozoans from the sample, removing all caprellids from that portion and counting them. The remaining unsorted bryozoans were then weighed, and the caprellid count from the sorted portion was extrapolated to the unsorted portion.

RESULTS

Caprellids were first collected in trawl samples on 9 March 2009 and observed in samples through 7 April 2009. During that period of time, 30 bay trawl and 30 dredge samples were collected. All caprellids collected during the observation period were attached to the bryozoan, *Bugula neritina*. Caprellids were observed in 11% of the bay trawls containing *B. neritina* and 30% of the oyster dredge samples containing *B. neritina*. Physicochemical measurements ranged from 15.8 – 22.3°C, 28.3 – 29.6 and 5.6 – 8.2 mg/L for water temperature, salinity, and dissolved oxygen, respectively.

Specimens were identified as *C. scaura* and *P. tenuis*. Of the samples containing caprellids, specimens of *C. scaura* were collected at all locations and *P. tenuis* was only collected at the Mesquite Bay site #077 (Figure 1). Both sexes, including gravid females were present in all samples. Densities of caprellids ranged between 0.1 – 3.4 individuals per gram of *B. neritina* (Table 1).

Distinguishing characteristics separating *C. scaura* from *P. tenuis* are quite noticeable. Adult males of *C. scaura* are much larger than those of *P. tenuis* (Figures 2, 3). Both sexes of *C. scaura* have a pronounced anteriorly directed spine on the cephalon where *P. tenuis* lacks any protrusion. *Paracaprella tenuis* has a distinct notch on the center of the palm of gnathopod 2 in the male, whereas *C. scaura* does not. *Caprella scaura* males have much longer antennae, head/pereonite 1 and pereonite 2 than *P. tenuis* (Figures 2, 3). Lastly, placement of gnathopod 2 is located posteriorly on pereonite 2 on male *C. scaura*, whereas it is located more anteriorly on

pereonite 2 for male *P. tenuis* (McCain 1968, Foster et al. 2004b; Figures 2, 3).

DISCUSSION

Other accounts of *C. scaura* and *P. tenuis* have noted no habitat selection (McCain 1968; Foster et al. 2004a; Foster et al. 2004b; Diaz et al. 2005; Krapp et al. 2006). However, all caprellids collected during this observation period were only associated with *B. neritina*. No caprellids were observed after early April, which coincided with a reduction in the presence of bryozoans in monthly bay trawls and oyster dredges. The use of bryozoans as habitat by caprellids may have been the mode of transportation and later introduction to the Aransas Bay ecosystem for these species.

Pederson and Peterson (2002) determined bryozoans to be an important transport mechanism for mobile benthos and young fishes in Biloxi Bay, Mississippi, with *P. tenuis* noted as one of the three most dominant species. Similarly, Keith (1971) found *Caprella californica* on *B. neritina* at significantly greater frequencies than on macroalgae. Another possible mode of expansion for *C. scaura* could have come from drifting sargassum by way of the GOM Loop Current, in combination with the seasonal southeast prevailing winds (Gower et al. 2006). However, during this study caprellids were only observed to be associated with bryozoan colonies. It is more likely an introduction occurred by way of ship hull fouling or ballast release of bryozoans. Aransas Bay is adjacent to the Port of Corpus Christi, which is the nation's fifth

largest port based on combined domestic and foreign trade tonnage (American Association of Port Authorities 2011).

At the time of manuscript submission, TPWD staff had collected an additional 640 trawl and dredge samples in the Aransas Bay ecosystem without observation of caprellids. During that time, the Texas coast received ample amounts of precipitation, resulting in a reduction of mean bay salinity from 34.0 to 14.0 (TPWD unpublished data). Similarly, collection of *B. neritina* has decreased since the last observation of caprellids. Winston (1977) described *B. neritina* as weakly euryhaline, not tolerating salinities below 18.0. It seems likely that *B. neritina* prefer or require greater salinities than those the estuarine environment can consistently provide. Because observations of caprellids only occurred in conjunction with *B. neritina*, it is likely that *C. scaura* and *P. tenuis* abundance was indirectly affected by lack of suitable habitat.

Observations noted in this study represent a range extension for *C. scaura* to the western GOM and provide valuable information regarding the distribution and abundance of both *C. scaura* and *P. tenuis* as there is no historical record of either species having been previously identified in the area based on TPWD's sampling program of more than 25 years. Because their occurrence has diminished, neither caprellid observed in Aransas Bay likely poses an immediate threat to other marine organisms occupying a similar habitat. The year round sampling conducted by TPWD will provide additional opportunities to monitor the occurrence of these and other caprellids along the entire Texas coast.

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EFFECTS OF A SEVERE COLD EVENT ON THE SUBTROPICAL, ESTUARINE—DEPENDENT COMMON SNOOK, *CENTROPOMUS UNDECIMALIS*

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ABSTRACT: The effects of infrequent disturbance events on marine fishes are often difficult to determine, due largely to lack of sufficient pre- and post-disturbance event data. In January 2010, subtropical southwestern Florida (USA) experienced extreme cold for 13 days, which caused extensive mortality of many fish species. The effect of this severe cold event on common snook (*Centropomus undecimalis*), an economically important gamefish, was assessed using three years (2007–2009) of pre-event and one year (2010) of post-event data from a tag-recapture program conducted over 28 km of Gulf of Mexico barrier islands of Florida. All metrics pointed to a significant effect of the severe cold event: post-disturbance apparent survival of marked fish was 96–97% lower than pre-disturbance, and post-disturbance common snook abundance was 75.57% and 41.88% less than in 2008 and 2009, the two years immediately pre-event. Although severe cold events have impacted subtropical Florida in the past, these events are infrequent (the previous recorded event was >30 years prior), and documentation of the impacts on common snook have not previously been published.

KEY WORDS: spawning habitat, survival, tag-recapture, thermal disturbance

INTRODUCTION

Disturbances play a fundamental role in shaping biological diversity (e.g., Cooper 1966, Connell 1978, Sousa 1979). Numerous non-mutually exclusive hypotheses have been proposed to explain how disturbances interact with competition, productivity, and life history strategies to maintain species abundance (e.g., Connell 1978, Huston 1994, White and Jentsch 2001). Given the importance of disturbances to biological organization, and the fortuitous nature of “natural experiments” provided by disturbances, studies that document ecological effects of disturbances are sorely needed.

With some notable exceptions (e.g., Sousa 1979, Hughes 1994, Syms and Jones 2000), studies of disturbances in marine systems have generally been opportunistic, whereby an ongoing study encompasses a disturbance event. Time-series are essential for drawing accurate pictures of species before a disturbance and determining the effects of the disturbance (Mackey and Currie 2001). For example, in a study of hurricane effects on coral reef fish assemblages, Adams (2001) first used a standard ‘before vs. after’ approach to data analysis, and found a decline in fish abundance and species richness after the hurricane. However, when the data were examined as a time series (17 months pre- and nine months post-hurricane census data), changes were shown to be long-term declines that were unaffected by the hurricane. Similarly, Lassig’s (1983) time series data showed little effect of a tropical cyclone on adult fishes, but a notable effect on recruits – findings likely unattainable with only data ‘snapshots.’ More recently, however, issues of temporal scale have been addressed as more multi-year datasets are becoming

available, and more studies have been able to address disturbances (e.g., Greenwood et al. 2006, Stevens et al. 2006). Multi-year studies provide data from before and after disturbance events that allow documentation of disturbance effects because the studies provide pre- and post-disturbance data.

Common snook, *Centropomus undecimalis*, is a tropical and subtropical, estuarine-dependent, euryhaline species that is ecologically and economically important throughout its range, especially in Florida (Taylor et al. 2000). Common snook are protandrous hermaphrodites, with sex ratio changing by size: < 553 mm standard length, the male:female ratio is ~1.9:1; at 553 mm the ratio is ~1:1; and at 750 mm the ratio is ~1:1.2 (Muller and Taylor 2006). The general life history is as follows: adult common snook spawn during summer in passes and inlets at the mouths of estuaries and along adjacent beaches (Taylor et al. 1998); larval planktonic stage is about 2 weeks (Peters et al. 1998); juvenile habitats are shallow, complex, meso- to oligohaline habitats (Peters et al. 1998), and adults use deeper estuarine and riverine habitats for overwintering (Blewett et al. 2009). Common snook in Florida can live for more than 20 yrs, with one to 7 yr olds being the most common age (Taylor 2000). The geographical distribution of common snook is restricted by temperature, with the northern edge of their range restricted by the 15°C winter isotherm; they stop feeding completely at 14.2°C, lose equilibrium at 12.7°C, and die at 12.5°C (Shafland 1983).

This manuscript reports the effects of a severe cold event on common snook in Florida (USA), using data gathered

from a multi-year study on snook movements on spawning grounds (Adams et al. 2009, 2011). After three years of study, an extended and severe period of cold temperatures impacted this subtropical region, causing extensive mortalities of common snook and many other fish species. Sampling that continued through the first year after the severe cold event allowed an estimate of the effects of the event on adult snook on spawning grounds.

MATERIALS AND METHODS

Study area

Charlotte Harbor is a 700 km² coastal plain estuarine system in southwest Florida, USA (Figure 1, Hammett 1990). The Peace, Myakka, and Caloosahatchee Rivers, and many smaller creeks throughout the drainage, transport large amounts of fresh water into the harbor. The climate is subtropical; mean seasonal water temperatures range from 12 to 36°C, and freezes are infrequent (Poulakis et al. 2003). The estuary is separated from the Gulf of Mexico (GOM) by a string of barrier islands, with tidal exchange through five inlets that separate the barrier islands—Boca Grande Pass, Captiva Pass, Redfish Pass, and Blind Pass within the study area, and San Carlos Pass south of the study area. The GOM shorelines of the islands are comprised entirely of sandy beaches. The passes are a mixture of natural sand and anthropogenically hardened shorelines. The passes and barrier island beaches are classified as spawning grounds during summer (May through September) (Taylor et al. 1998, AJA pers. obs.).

Severe Cold Event

On 2 January 2010, a severe cold front followed by a reinforcing high pressure arrived in south Florida, creating abnormally cold conditions for 13 d. Daytime air temperatures were about 9°C below normal, and extended northerly winds kept temperatures low and caused water temperatures throughout the estuary to drop well below normal. Hourly water temperatures, averaged from 4 sensors from the Sanibel–Captiva Conservation Foundation Marine Laboratory's River, Estuary and Coastal Observing Network (SCCF RECON) (Figure 1), revealed that water temperature dropped from about 18°C on 1 January to 12°C by 6 January, and remained below 12°C through 16 January (Figure 2). This was well below the mean winter water temperature of 21°C for the estuary, and below the lethal thermal threshold of common snook (12.5°C) for at least 10 d. Severe cold events are infrequent but recurring in

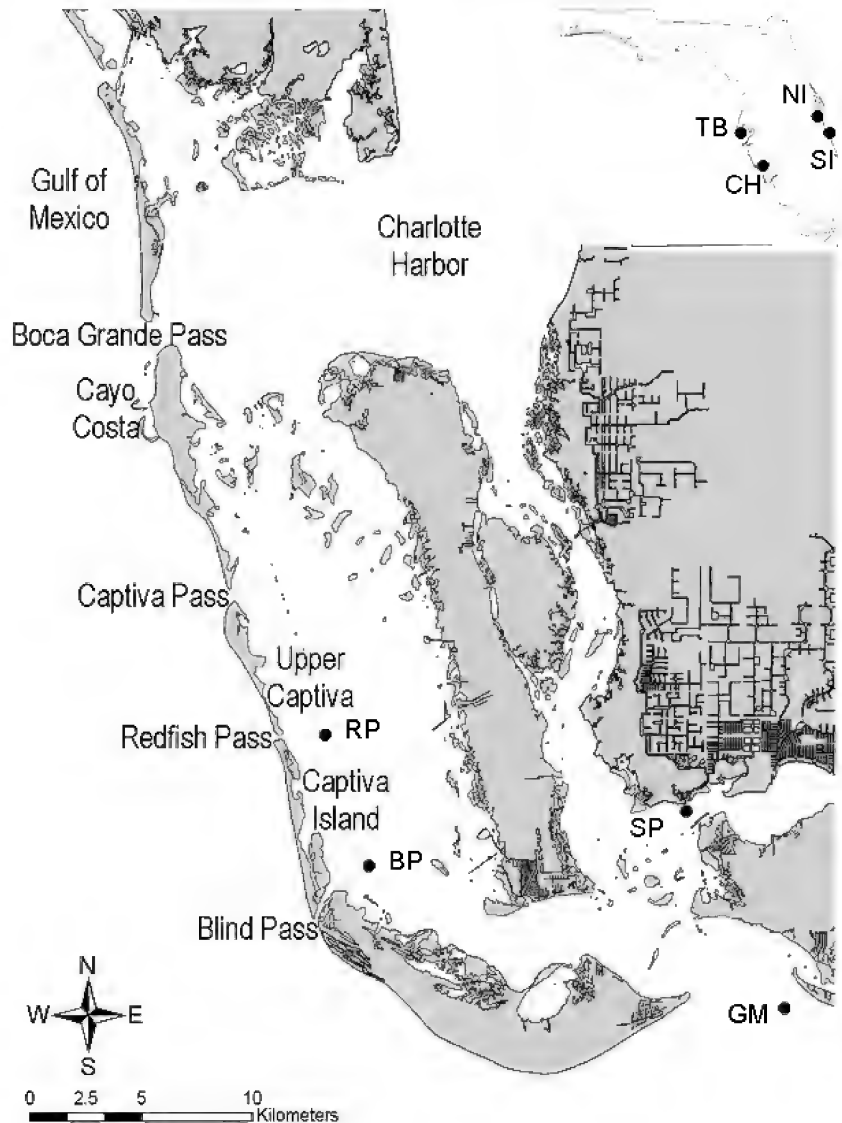


Figure 1. Map of the Charlotte Harbor (CH) study area in southwestern Florida, USA. Tag and recapture by seine occurred along barrier island beaches from the northern end of Cayo Costa (at Boca Grande Pass) to the southern end of Captiva (at Blind Pass). Four SCCF RECON monitoring stations (Redfish Pass (RP), Blind Pass (BP), Shell Point (SP) and Gulf of Mexico (GM)) were used to obtain water temperatures for January 2010. The other estuaries sampled by Florida Fish and Wildlife Conservation Commission Fisheries Independent Monitoring program (see inset) are Tampa Bay (TB), North Indian River Lagoon (NI), and South Indian River Lagoon (SI).

Florida, with multiple historical reports (e.g., Storey 1937). Though there has usually been at least one severe cold disturbance per decade recorded for terrestrial ecosystems (Miller and Downtown 1993), the most recent documented marine cold event of similar magnitude to the 2010 disturbance was in 1977 (Gilmore et al. 1978, Bohnsack 1983), and prior to that in 1940 (Galloway 1941), both of which caused significant fish mortalities. Few published reports document more than a species list of mortalities (but see Gilmore et al. 1978, Bohnsack 1983).

Sampling protocol

As part of a study to examine levels of site fidelity of adult common snook to spawning grounds (Adams et al. 2009, 2011), adult snook were captured by seine along GOM beaches of Florida during the summer spawning season from 2007 through 2010. Tag–recapture methods were used to estimate common snook use of spawning grounds within and among years. Snook exhibited >97% fidelity to spawning grounds over this 4 y time period (Adams et al. 2009, 2011). In this paper we compare 3 years of seine and tag–recapture data from prior to the severe cold event (2007 – 2009) to one year of data after the event (2010) to estimate the effects of the cold event on abundance of adult common snook on the spawning grounds.

During the summer spawning season from 2007 through 2010, adult common snook were sampled with seine nets along beaches of 3 barrier islands – Cayo Costa (12.4 km long), Upper Captiva (8 km), and Captiva (8.9 km) – between Boca Grande Pass and Blind Pass (Figure 1). Sampling occurred from May through September in 2007 and from May through August of 2008 through 2010. Sampling effort was similar among years and islands (Table 1).

Sampling procedures were carried out according to Adams et al. (2009). To summarize, sampling occurred between 0700 hrs (onset of suitable sunlight for sighting fish) and 1200 hrs. Sampling did not take place after 1200 hrs due to increase in the volume of human activity on beaches and water temperatures that reached stressful levels for common snook. Sampling occurred as conditions allowed – onshore winds or high surf prevented sampling, as did proximity of hurricanes – and did not focus on a particular lunar phase. On each sample day, the entire length of beach that could be sampled on each island (e.g., free of trees and other debris) was searched if time allowed. A shallow–draft boat was used to set seine nets around schools of common snook that were spotted along the beach. The procedure was to steer the boat along the beach and, when common snook were spotted, one end of the net was deployed off the back of the boat and the boat was used to set the net around the school. Dur-

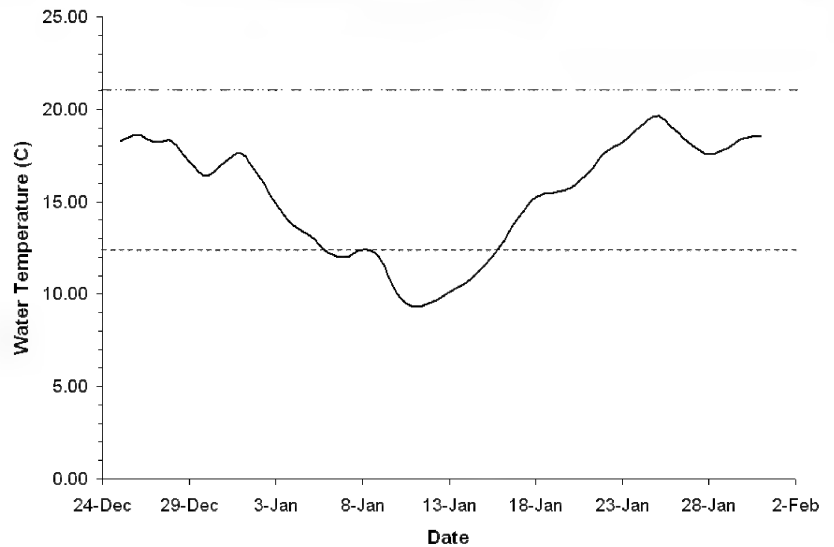


Figure 2. January 2010 water temperature in Charlotte Harbor. Water temperature was averaged from hourly readings from 4 SCCF RECON sensors (Shell Point, Redfish Pass, Blind Pass, GOM; see Figure 1). The upper dashed line is the mean winter water temperature in Charlotte Harbor (21°C) and the lower dotted line is the lethal temperature threshold of the common snook (12.5°C).

ing summer, common snook are typically found within 2 m of shore, so this method is very effective. Three center–bag seine nets were used during this study: 91.44 m x 2.44 m with 19.05 mm mesh was used in 2007 and 2010; 182.88 m x 2.44 m with 15 mm mesh was used in 2007, 2008, 2009; and 152.40 m x 2.44 m with 35 mm mesh was used in 2007 and 2010. The nets were hauled onto shore, and the fish captured in the center bag. Once captured, the common snook were placed in mesh holding pens until tagged.

The number of samples per day ranged from one to 7 and depended on the number of common snook spotted and captured. For example, if a large number of common snook was captured in a sample, the time to measure and tag the fish reduced the amount of time available for more samples on that day. On days in which few common snook were spotted, the net was set ‘blind’ (i.e., set without seeing fish) to ensure samples were obtained on that day.

Tag–Recapture

Tagging. Prior to tagging, common snook were removed from the holding pens and placed in a cooler with a seawater and Alka–Seltzer mix (1–1.5 tabs/4 L seawater) to immobilize the fish. Once immobilized, a 23 mm HDX Passive Integrated Transponder (PIT) tag (TIRFID 2000, Texas Instruments) with a unique 16–digit identification number was inserted into the abdominal cavity through a 3 mm incision (*sensu* Adams et al. 2006). Additionally, during 2007 through 2009, common snook were also marked with external T–bar anchor or dart tags (Floy Tag and Manufacturing) to increase probability of angler recapture. Standard length (SL) in millimeters, PIT and external tag number, and latitude–longitude were recorded for each fish. After tagging, fish were

TABLE 1. Number of sampling days by island and year.

Island	Year				Total
	2007	2008	2009	2010	
Cayo Costa	12	7	8	15	42
Upper Captiva	13	7	13	15	48
Captiva	8	7	7	11	33
Total	33	21	28	41	123

placed in a recovery pen for about 5 minutes and released at the site of capture. Tagging experiments with juvenile snook reported low or no mortality (Adams et al. 2006), so post-tagging mortality in this study was assumed to be minor. Of the 3,315 snook tagged during this study, one post-tagging mortality occurred in the recovery pen. A necropsy was conducted and there were no apparent signs of injury due to tag insertion, disease or macro-parasitic infection.

Recapture. Recapture occurred by seine during tagging efforts along the GOM beaches of the barrier islands, and by recreational anglers using hook and line. During seine sampling and prior to tagging, all common snook were scanned with an Allflex ISO compatible RFID portable reader for PIT tags (model number RS601, Allflex). In addition, on numerous sampling days common snook were not tagged, and all captured fish were scanned for tags and released. For recaptures, SL, PIT tag number, and latitude–longitude were recorded and the fish were released. Three Allflex RFID portable readers were also distributed to local recreational fishing charter captains who frequently targeted common snook. If PIT tags were detected, the guides recorded location of the recapture, length of the fish and the PIT tag identification number. Only 3 PIT tagged common snook were recaptured by these charter captains. Recreational anglers who caught common snook with external tags reported the catch to the phone number listed on the tag, and provided tag identification number, length of the fish, and the location of capture.

Data Analysis

Three different metrics were used to compare pre- and post-cold event data: apparent survival, length–frequency, and catch (expressed as abundance). Apparent survival ($1 - (\text{mortality} + \text{emigration})$) was calculated between each summer for $n = 3,275$ marked fish (41 marks were found to be mislabeled in the tagging database, and therefore excluded from survival analysis). We combined marking information with recaptures from seine netting and angler recaptures near spawning grounds ($n = 211$: 189 seine net recaptures; 22 angler recaptures) from May to September and created a capture history for each marked fish. Capture histories were constructed on a yearly basis (2007, 2008, 2009, 2010), with fish being assigned a ‘1’ in years they were marked or recaptured, and a ‘0’ in years they were not seen. To analyze

the data, a Cormack–Jolly–Seber open population model (Cormack 1964, Jolly 1965, Seber 1965) was used in the computer program MARK (White and Burnham 1999). The Cormack–Jolly–Seber model calculates 2 parameters: (1) apparent survival probability ($\Phi = 1 - \text{mortality} - \text{emigration}$), and (2) capture probability (p). Unique apparent survival values were calculated between each year in order to investigate the impact of the disturbance on survival of common snook that used the study area as spawning grounds. Capture probability was kept constant as the same sampling methods were used each year, which likely resulted in a nearly identical probability of capturing fish present during sampling. Lower survival between the summer of 2009 and the summer of 2010 as compared to previous years would indicate a significant effect of the severe cold event.

Fish length frequencies were \log_{10} transformed and examined by year with ANOVA to determine whether snook size differed between pre- and post-cold event years. Abundance (number of common snook per 100 m of shoreline) was calculated as the number of individuals caught per day over the total length of beach sampled that day (length of net \times number of sets). Combining all samples from a day reduced the problem caused by zero catches (especially high in 2010), which precluded reasonable statistical approaches. To determine whether the different nets resulted in different catch rates, we compared common snook abundance (number of snook per 100 m of shoreline sampled) for different nets used within the same year. The comparisons were: 91.44 m \times 152.4 m in 2007 and 2010; 91.4 m \times 182.8 m in 2008. There was no comparison of gears in 2009 because only the 182.8 m net was used. For each comparison, we used a one-way ANOVA on log transformed abundance (number of snook per 100 m of shoreline). If results were nonsignificant for each comparison, we combined abundance data from all nets for analysis. We used a two-way ANOVA to determine whether abundance differed by year and island, with a focus on whether abundance in 2010 differed from previous years on all islands.

RESULTS

Samples were conducted over a total of 123 d during the 4 year study (Table 1). Abiotic parameters were well within requirements for common snook spawning in all years (Table 2). All metrics indicated a significant negative effect of the severe cold event.

The Cormack–Jolly–Seber apparent survival estimates for the first 2 years validate the model by aligning with the mortality estimates used in the most recent stock assessment for common snook (see Figure 4.3.2.3 in Muller and Taylor 2006). In this study, apparent survival dropped substantially from 0.45 (upper 95% Confidence Interval = 0.23, lower 95% CI = 0.21) and 0.65 (upper 95% CI = 0.26, lower 95% CI = 0.39) for the years prior to the cold event, to 0.01 (upper 95% CI = 0.05, lower 95% CI = 0.01) for the time period

TABLE 2. Mean (\pm SE) of dissolved oxygen, water temperature and salinity recorded during net sampling from May through August of each year.

Year	Dissolved Oxygen (mg/L)	Water Temperature (°C)	Salinity
2007	6.20 \pm 0.09	30.00 \pm 0.22	36.71 \pm 0.07
2008	5.80 \pm 0.11	29.96 \pm 0.28	35.63 \pm 0.03
2009	5.44 \pm 0.05	30.29 \pm 0.40	36.59 \pm 0.25
2010	5.46 \pm 0.06	29.84 \pm 0.09	34.66 \pm 0.06

encompassing the cold event (i.e., 2009 to 2010). The 96–97% decrease in apparent survival indicates that few common snook returned to the spawning grounds in the spawning season that followed the cold event. The significant difference in length by year (ANOVA on \log_{10} transformed SL: $F_{3,3310} = 53.993$, $p < 0.001$, Figure 3) was not associated with the cold event, but was instead due to a relatively larger size distribution in 2007, followed by a decrease in 2008 and 2009.

Results of gear comparisons were nonsignificant: 91.4 m x 152.4 m in 2007 ($F = 0.516$, $p = 0.482$); 91.4 m x 152.4 m in 2010 ($F = 0.509$, $p = 0.48$); 91.4 m x 182.8 m in 2008 ($F = 0.11$, $p = 0.744$) and thus abundance data were combined for all nets. There was a Year x Island interaction effect for the analysis of log transformed abundance (number of common snook per 100 m of shoreline) (Table 3). However, on all islands abundance was lowest in the year following the cold event when compared to previous years (Figure 4). Therefore, we focused on the abundance estimates for all islands combined. For all islands combined, non transformed abundance in 2010 was 75.57% and 41.88% lower than in 2008 and 2009. The Florida Fish and Wildlife Conservation Commission (FWC) Fisheries Independent Monitoring sampling program saw similar trends in multiple estuaries (Table 4) (FWRI 2010). In addition, one author (AJA) counted 1,132 dead, floating adult snook in a known wintering location (about 1 ha) at the end of the cold event. Conversations with numerous recreational fishermen suggested that some snook may have died during the weeks following the cold event; they reported seeing common snook with external lesions and fungal growth during this time period. Statewide data collected by FWC also indicated significant mortalities of other species, with more than 27 species reported killed on the FCW Fish Kill Hotline (<http://research.myfwc.com/fishkill/>), representing 21 families (see Appendix A).

DISCUSSION

The severe cold event of January 2010 had a major effect on common snook in southwest Florida. There was a 96–97% post-cold event decrease in apparent survival estimates and a 41.88% decline in nominal abundance from

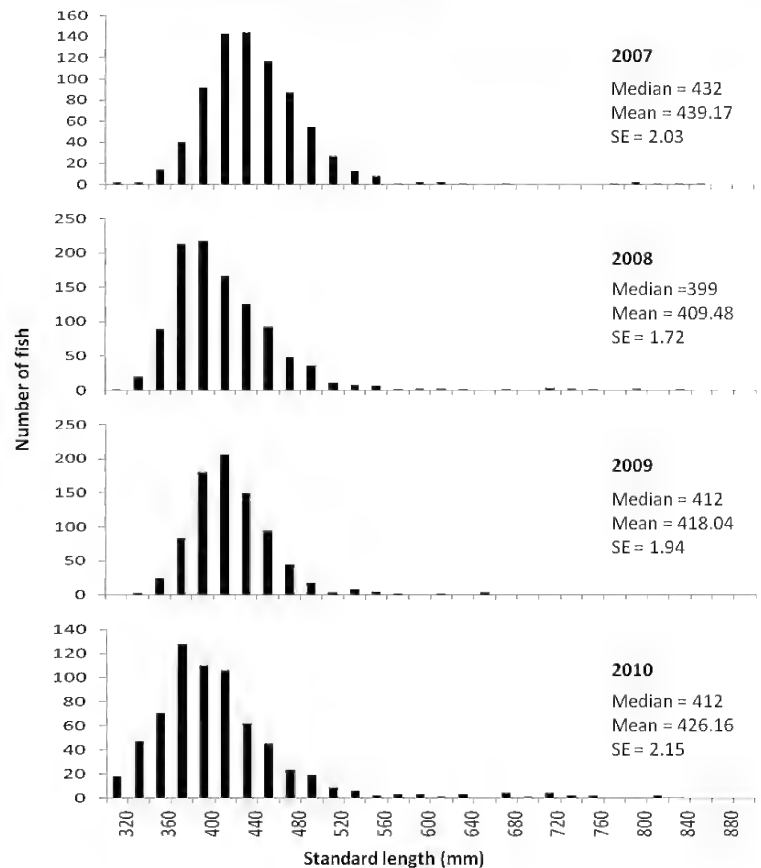


Figure 3. Size frequency of common snook by year for all islands combined. SE = standard error.

2009 and a 75.57% decline from 2008. The event appeared to affect all sizes classes sampled in spawning grounds similarly, suggesting a widespread effect on adults. That all of the metrics examined in this study show the same trend provides a compelling argument for a strong negative effect of the cold event. Moreover, although the estimates of abundance are somewhat confounded by an increase in blind sets in the post-disturbance year, this in itself is a strong indicator of the extremely low abundance of common snook after the cold event.

The clumped distribution of common snook on spawning grounds during the spawning season likely biased our data toward underestimating abundance declines, suggesting that even though we found a major effect, our findings are likely conservative. This is because analyzing abundance based on aggregating fish can be misleading as the numbers are prone to hyperstability (Sadovy and Domeier 2005). Hyperstability occurs with fish that commonly aggregate, because an aggregation that is repeatedly targeted or sampled continues to result in high catches even though the overall abundance may have declined. The northern cod, *Gadus morhua*, fishery, for example, had an increasing catch-per-unit-effort while, in fact, the population was being overfished for decades (Rose and Kulka 1999) because of this bias.

TABLE 3. Summary of a two-way ANOVA by year and island on \log_{10} transformed abundance.

Source	SS	df	MS	F	P
Year	3.134	3	1.045	19.529	<0.001
Island	2.565	2	1.283	23.979	<0.001
Year x Island	0.851	6	0.142	2.65	<0.05
Error	5.082	95	0.053		

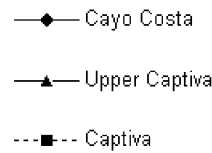


Figure 4. Log abundance (number of common snook per 100 m of shoreline) by year and island. Values are means \pm standard error. There was a significant year \times island interaction effect (Table 3), but this interaction was not associated with the cold event. The vertical line between 2009 and 2010 indicates the occurrence of the severe cold event.

It is not possible to partition mortality and emigration in the calculation of apparent survival for this study, so we suggest two possible causes for the decline in common snook abundance on spawning grounds – lethal and sublethal effects. In either case, the cold event caused a severe reduction in abundance of common snook on spawning grounds in the year following the cold event.

We suggest that lethal effects resulting from thermal stress from the severe cold was the primary cause of the decline of adult common snook on spawning grounds. Immediate lethal effects likely occurred for common snook when water temperature dropped below their lower thermal limit (12.5°C) for 10 d, leading to cellular functions ceasing and, ultimately, mortality. Although it is possible that some common snook found thermal refuges (e.g., freshwater springs of constant temperature) in which the water temperature did not reach lethal levels, reports of dead common snook were frequent and widespread during and immediately following the cold event, indicating extremely high, immediate lethal effects. The data from the FWRI (2010) report also support the argument that lethal effects were the dominant cause for the observed decline in common snook abundance on spawning grounds. It is also likely that the ability of common snook to avoid predators (sharks, dolphins, birds) was also compromised; when declining water temperatures approach the lethal limit of 12.5°C , common snook become very lethargic and lose some of their mobility, thus making them more susceptible to predation. Finally, delayed lethal effects, such as reduced immune response due to stress, may have also contributed to common snook mortalities caused by the

cold event.

A probable secondary cause of adult common snook abundance decline on spawning grounds was sublethal effects. Sublethal effects occur when fish survive a stressful event, but experience reduced fitness that impairs processes such as spawning. In this scenario, surviving common snook most likely utilized available resources to fortify their immune systems, contribute to somatic growth, and to counter other stress-related effects that impacted their reproductive fitness (Schreck et al. 2001). This leaves fewer resources to allocate to spawning, which can result in no or a severely reduced spawning season for these individuals (McCullough et al. 2001). The scenario of skipping a spawning season is somewhat likely for common snook as even in normal years only a portion of the mature population spawns (Blewett 2009). Similarly, individuals of barramundi,

Lates calcarifer, a Pacific species with a similar life history, do not spawn in every year (Milton 2005). Spawning can be a stressful event for fishes resulting in death for individuals of some species (e.g., Pyron and Beitingner 1993), and progeny of physiologically stressed fishes are often deformed or have low survival (McCullough et al. 2001). Therefore, investing in somatic rather than gonadal growth may be an effective bet-hedging strategy for the common snook, especially following a disturbance.

Alternatively, the observed decline in common snook abundance on spawning grounds may have been caused by common snook moving to other locations. For example, it might be argued that abiotic conditions on the spawning grounds in the year following the cold event may not have been suitable for spawning. During this study, however, water temperature, salinity and dissolved oxygen on the GOM beaches during the summer months following the severe cold event had little variation and were within the required

TABLE 4. Catches of common snook, *Centropomus undecimalis*, by Florida Fish and Wildlife Conservation Commission Fisheries Independent Monitoring program for 4 estuaries. See Figure 1 for locations. Values are total number of common snook captured during January through June of each year.

Year	Location			
	Tampa Bay	Charlotte Harbor	North Indian River Lagoon	South Indian River Lagoon
2008	639	223	190	341
2009	347	123	144	449
2010	90	28	30	154

physiological range of common snook (Table 3; Peters et al. 1998), so were not likely factors influencing the decrease in abundance of the common snook on the summer spawning grounds. In addition, since we sampled 28 km of coastal beach habitat, we would have detected long-distance movement as well as any tendency toward increased dispersal over time or with fish size. Even if common snook dispersed to other spawning locations outside the study area, for example, if such movement was common it would have also resulted in movements among islands sampled in this study, but such movement was rare.

It is also possible that common snook that previously spawned along beaches moved offshore to spawn in the year following the cold event. Common snook apparently also spawn on offshore reefs (Taylor et al. 1998), habitats which were not sampled in this study. However, if this occurred, this would still be considered a major effect of the cold event in that the location of spawning changed dramatically for a large portion of the adult population. This is significant because hydrodynamic conditions affecting larval distribution would differ between the beach spawning grounds and purported offshore locations. One would expect a spawning site to, on average, provide larvae to a particular location, thus connecting specific spawning and nursery habitats. If this area contains suitable nursery habitat, then that spawning location can expect some reproductive success. On the other hand, if the larval settlement area contains no or poor quality nursery habitat, then reproductive success of that spawning site will be low. Therefore, under this scenario, a change in spawning location might impact recovery due to a change in coastal habitats that receive common snook larvae.

The decline in common snook abundance from 2008 to 2009, prior to the disturbance, might indicate that other factors are influencing regional populations. However, the extensive reports of region-wide common snook mortalities associated with the cold event, reports from recreational fishermen of low common snook catch rates in the year af-

ter the cold event, and the rather dramatic decline in abundance in the year following the cold event suggest that the disturbance effect was severe even in the context of a possible longer term trend of population decline. If other factors are also influencing common snook abundance over the longer term, these factors may synergistically interact with the disturbance to affect the recovery trajectory of the common snook population.

Infrequent, severe cold disturbances recur regularly in subtropical southwest Florida, with published reports of cold-related fish kills from as early as the 1800's (e.g., Storey 1936, Galloway 1941). More recently, notable cold disturbances occurred in 1977 (Gilmore et al. 1978, Bohnsack 1983) and throughout the 1980's (Miller and Downtown 1993), though not all appear to have impacted fishes. However, these events generally occur infrequently enough that the common snook population has been able to recover to pre-event levels before the next cold event occurs (Storey and Gudger 1936).

Since common snook exhibit nearly 100% site fidelity to spawning grounds (Adams et al. 2009, 2011), there may be spawning-based population segregation that effectively creates numerous smaller spawning populations distributed along the coastline, which may affect recovery. Too few tagged common snook were recaptured in 2010 to determine whether the disturbance altered their site fidelity behavior, but continued study of the response to this disturbance would address that issue. Spawning site fidelity may slow recovery from disturbances; the slower than expected response of Atlantic cod may be in part due to a greater degree of spawning segregation than had been recognized, because site fidelity impedes recolonization of spawning grounds (Robichaud and Rose 2001). The degree to which this will occur is likely linked to the type of spawning site fidelity exhibited by common snook (philopatry, spawning-group fidelity, or socially learned fidelity). As this mechanism is of yet unknown for common snook it should be a focus for future studies.

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APPENDIX A. List of fishes killed by the January 2010 cold event reported to the Florida Fish and Wildlife Conservation Commission Fish Kill Hotline (<http://research.myfwc.com/fishkill>).

Family	Species
Elopidae	<i>Elops saurus</i>
Megalopidae	<i>Megalops atlanticus</i>
Albulidae	<i>Albula</i> spp.
Clupeidae	unidentified
Ariidae	unidentified
Mugilidae	<i>Mugil</i> spp.
Atherinidae	unidentified
Belonidae	unidentified
Serranidae	<i>Epinephelus</i> spp. <i>Mycteroperca</i> spp.
Carangidae	<i>Caranx hippos</i> <i>Seriola dumerili</i> <i>Trachinotus carolinus</i> <i>Trachinotus falcatus</i>
Lutjanidae	unidentified
Gerreidae	<i>Diapterus plumieri</i>
Haemulidae	unidentified
Sparidae	<i>Archosargus probatocephalus</i> <i>Lagodon rhomboides</i>
Sciaenidae	<i>Cynoscion nebulosus</i> <i>Sciaenops ocellatus</i>
Pomacanthidae	unidentified
Scaridae	unidentified
Sphyraenidae	<i>Sphyraena barracuda</i>
Ostraciidae	unidentified
Tetraodontidae	unidentified

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Early Growth of Three Kingfish (*Menticirrhus*) Species Found in Coastal Waters of the Northern Gulf of Mexico

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EARLY GROWTH OF THREE KINGFISH (*MENTICIRRHUS*) SPECIES FOUND IN COASTAL WATERS OF THE NORTHERN GULF OF MEXICO

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ABSTRACT: Southern kingfish (*Menticirrhus americanus*), gulf kingfish (*M. littoralis*), and northern kingfish (*M. saxatilis*) are members of the drum family (Sciaenidae) that are widespread in coastal habitats of the western Atlantic, including in the Gulf of Mexico (GOM). Despite their economic and ecological importance, little is known about growth of young kingfish. Young kingfish were collected from four different Mississippi shoreline habitats in 2005 and 2006; two associated with barrier islands and two along the mainland. Barrier island habitats included surf zones on the south shore and grass beds on the north shore. Mainland habitats were located along marsh-edges and sandy shorelines. Kingfish growth comparisons were made using analysis of covariance (ANCOVA) on 194 aged fish (127 *M. americanus*, 54 *M. littoralis*, and 13 *M. saxatilis*). Growth rates for all three species were generally similar ranging from about 0.7mm/day at 4–6 mm standard length (SL) to 1.9mm/day at 55–60mm SL. In 2005, *M. americanus* from marsh-edges grew significantly faster than those from sandy shorelines. Size-at-age of *M. americanus* and *M. littoralis* was significantly smaller in the spring than in the summer and fall, while both growth rate and size-at-age were similar in the summer and fall.

KEY WORDS: *Menticirrhus americanus*, *Menticirrhus littoralis*, *Menticirrhus saxatilis*, growth rate, size-at-age

INTRODUCTION

Southern kingfish (*Menticirrhus americanus*), gulf kingfish (*M. littoralis*) and northern kingfish (*M. saxatilis*) co-occur in littoral habitats of the northern Gulf of Mexico (GOM) where they are important demersal members of the coastal ecosystem. In U.S. waters, *Menticirrhus americanus* and *M. littoralis* are common in the GOM and along the south Atlantic coast, whereas *M. saxatilis* are more common along the northeast coast and not as common in the GOM (Irwin 1970). Young *M. americanus* occur in surf zones of barrier islands, in coastal bays and along marsh-edges. Unlike the other kingfish, young *M. littoralis* occur almost entirely in surf zones of barrier islands (Modde and Ross 1981, Ross et al. 1987). Young *M. saxatilis* also can occur in surf zones and have been reported to enter bays (Bearden 1963, Schaefer 1965). Spawning of all three species occurs in the shallow GOM from spring to early fall (Miller 1965, Irwin 1970, Johnson 1978, McMichael and Ross 1987).

Much of what is known about kingfish growth is based on adult length–frequency data (Hildebrand and Cable 1934, Springer and Woodburn 1960, Bearden 1963, Fritzsche and Crowe 1981, Crowe 1984, Harding and Chittenden 1987), measurements of scale annuli (Schaefer 1965, Smith and Wenner 1985), and tag/return data (Miller et al. 2002). The current study is the first to use otoliths as a method for aging and comparing the growth of the three young kingfish species.

The purpose of this study was to determine growth patterns of young kingfish (4–60 mm standard length, SL) collected from barrier island surf zones and grass beds, and mainland marsh-edges and sandy shorelines in coastal Mississippi. Comparisons were made among the 3 species, in-

ter-annually, seasonally, and among different habitats in an effort to better understand early growth histories of kingfish.

MATERIALS AND METHODS

Field sampling

Sampling began in April and extended through November in 2005 and 2006. Four habitat types were sampled monthly with each habitat type represented by 2 sites (8 stations). Surf zone and grass bed sites were located along the south and north sides, respectively, of Horn Island, a barrier island 22 km long and about 1.2 km wide located about 10 km off the Mississippi coast (Figure 1). Barrier island surf zone sites were located near the west tip and middle portion of the south side of the island (stations 4 and 8). Barrier island grass bed sites (3 and 7) were located near the west tip and middle portion of the north side of the island; *Halodule wrightii* was the dominant submerged seagrass. Mainland marsh edge sites (1 and 5) were fringed with *Juncus roemerianus* and were located near the mouths of Davis Bayou, MS and the east branch of the Pascagoula River. Mainland sandy shoreline sites (2 and 6) were located at Bellefontaine, MS and Pascagoula, MS beaches. Offshore surf zone sites were also characterized by a sandy shoreline, but we use the designation sandy shoreline only for mainland sites with a sandy shoreline. Collections were taken at each site during each sampling event with a 7.5 m bag seine fitted with 3.2 mm mesh and a beam plankton trawl (BPL) with 1.6 mm mesh wings and a 750 μ m cod-end. Surface water temperature was measured at each collection location with a YSI Model 55. Specimens were stored in labeled containers and placed on ice for transport to the laboratory. In the

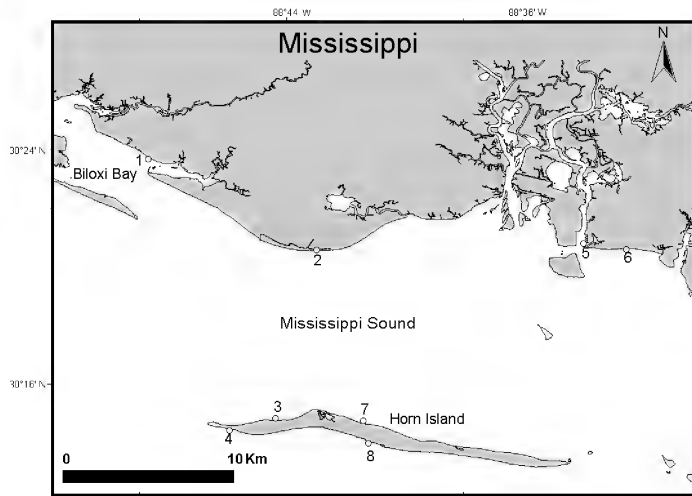


Figure 1. Sample locations along the Mississippi Gulf Coast included marsh edge (sites 1 and 5), sandy shoreline (sites 2 and 6), grass bed (sites 3 and 7) and surf zone habitats (sites 4 and 8). Numbers indicate sampling sites.

laboratory, kingfish were identified to species, measured to the nearest mm SL and preserved in 95% ethanol. Supplemental seine collections were taken during the summers of 2005 and 2006 from each habitat type to provide additional samples for otolith analyses.

Otolith preparation and analysis

For otolith analyses, kingfish were divided into 10 mm size increments over a size range of up to 60 mm SL. A minimum of 2 specimens of each species was randomly selected from each of the 6 size increments. Specimens were taken from all habitats and months when available. When a species was not common from a habitat, all available specimens were analyzed from that habitat. Growth rates of young kingfish were based upon SL and the number of daily otolith growth increments. Daily periodicity of increment formation has not been validated for the 3 *Menticirrhus* species, but has been validated for early life stages of 4 other Gulf sciaenids including *Sciaenops ocellatus* (Comyns et al. 1989), *Cynoscion nebulosus* (Peebles and Tolley 1988), *Micropogonias undulatus* (Nixon and Jones 1997), and *Leiostomus xanthurus* (Siegfried and Weinstein 1989). Because the growth increment formation for the kingfish resembles that of other sciaenids, it was presumed increments were formed daily.

The left sagittal otolith was removed from each specimen, embedded in a resin block, and a thin cross-section containing the otolith primordium was prepared in the transverse plane following Secor et al. (1992). Otolith increments were counted using an Olympus compound microscope and a second blind reading was made at a later date. Otoliths having conflicting readings were read a third time by 2 readers, and if a consensus could not be reached, the otolith was excluded. Right sagittal otoliths were used if the left was damaged or unreadable. A comparison of left and right otolith diameters with a paired t-test (SPSS 15.0) for *M. americanus* showed no significant difference between di-

ameters of left and right sagittal otoliths ($n = 18$, $p = 0.40$).

To determine the best relationship for describing kingfish age-length relationships, age-length data were fitted with a power curve, an exponential curve, and a linear regression. A power curve described by the equation $SL = aA^b$ [where $a = Y$ -intercept of the functional regression, A = age in days, and b = slope of the regression line (instantaneous growth rate)] provided the best fit. To meet assumptions of normality and homogeneity of variance the linearized form of the power curve was used: $\ln(SL) = \ln(a) + b * \ln(A)$. Linearized regressions were compared by species, seasons, years, and habitats when sufficient sample sizes were available using an analysis of covariance (ANCOVA, SPSS 15.0), with log-transformed age as the covariate. To analyze differences in growth, both growth rates (regression slopes) and size-at-ages (adjusted group means) were assessed as potentially separate influences on the early growth histories. First, growth rates were tested for significant difference, and if there was not a difference in growth rates, then size-at-ages were tested. The Bonferroni sequential procedure was used to control for type I errors when 3 pair-wise comparisons were made. Where heterogeneous slopes precluded conventional ANCOVA, slopes of linearized age-length relationships were compared using the GT2-method which generates 95% comparison intervals among a set of regression coefficients (Sokal and Rohlf 1995). In order to compare growth of kingfish species by seasons, kingfish were classified as being collected during spring (April–May), summer (June–September), or fall (October–November).

RESULTS

Kingfish growth comparisons were made on 194 aged fish (127 *M. americanus*, 54 *M. littoralis*, and 13 *M. saxatilis*) which showed increasing growth with increasing size and warmer water temperatures. Water temperature varied annually with mean station water temperature 1.4 to 3.3°C lower in 2005 than in 2006 (Figure 2).

All growth slopes were homogeneous ($p > 0.05$) except comparison of marsh and shoreline habitats (see below). Interspecific comparisons of growth rates did not reveal

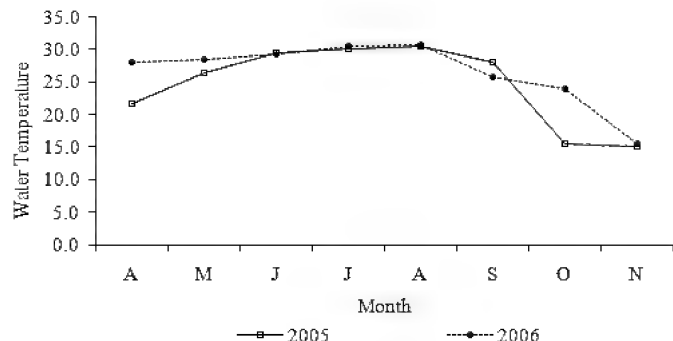


Figure 2. Mean monthly water temperature (°C) from stations during the study period (April–November) in 2005 and 2006.

TABLE 1. An analysis of covariance (ANCOVA) of log-transformed kingfish standard length (SL) and log-transformed age as the covariate was used in comparisons of kingfish growth among species, year, season, and habitat. A. Regressions, sample size (n), slopes, and standard error (SE). B. ANCOVA regression comparison(s) and significance values for slopes and adjusted group means.

A.				B.		
Regressions	n	Slope	SE	ANCOVA Regression Comparison(s)	Slope Sig.	Adjusted Group Means Sig.
Species (2005)				1, 2	0.790	0.116
1 <i>M. americanus</i>	63	1.736	0.069			
2 <i>M. littoralis</i>	15	1.699	0.075			
Species (2006)				3, 4, 5	0.644	0.062
3 <i>M. americanus</i>	64	1.686	0.040			
3 <i>M. littoralis</i>	39	1.617	0.068			
5 <i>M. saxatilis</i>	13	1.707	0.041			
Year (<i>M. americanus</i>)				6, 7	0.154	0.327
6 2005	29	1.591	0.070			
7 2006	45	1.709	0.041			
Year (<i>M. littoralis</i>)				8, 9	0.237	0.010
8 2005	12	1.723	0.079			
9 2006	17	1.589	0.076			
Season (<i>M. americanus</i>)				10, 11, 12	0.370	<0.001
10 Spring 2005	13	1.688	0.173	10, 11		<0.001
11 Summer 2005	33	1.607	0.087	10, 12		<0.001
12 Fall 2005	17	1.412	0.114	11, 12		0.087
Season (<i>M. littoralis</i>)				13, 14, 15	0.323	<0.001
13 Spring 2006	11	1.711	0.095	13, 14		<0.001
14 Summer 2006	20	1.562	0.060	13, 15		<0.001
15 Fall 2006	8	1.470	0.117	14, 15		0.240
Habitat (<i>M. americanus</i>)				16, 17	*	
16 Marsh-edge 2005	24	2.041	0.128			
17 Sandy shoreline 2005	39	1.585	0.073			
Habitat (<i>M. americanus</i>)				18, 19	0.360	0.050
18 Marsh-edge 2006	30	1.741	0.053			
19 Sandy shoreline 2006	34	1.669	0.075			

* Slopes were heterogeneous so the age-length relationships were compared using the GT2-method which generates 95% comparison intervals among a set of regression coefficients (Sokal and Rohlf 1995).

any significant differences between species. In 2005, only *M. americanus* and *M. littoralis* were collected in sufficient numbers for an interspecific comparison of growth. Growth of the 2 species was similar, with no significant difference in growth rate or size-at-age (ANCOVA, $p = 0.116$, Table 1). Similarly, no significant differences in growth rates or size-at-age relationships (ANCOVA, $p = 0.062$, Table 1) were found in kingfish collected in 2006. Mean growth rates of all 3 species were similar and ranged from about 0.7 mm/day at 4–6 mm SL to 1.9 mm/day at 55–60 mm SL.

Interannual comparisons of growth rates were made for *M. americanus* and *M. littoralis* collected during the summers of 2005 and 2006. *Menticirrhus americanus* growth rates and size-at-age in 2005 and 2006 were not significantly different (ANCOVA, $p = 0.327$, Table 1). However, size-at-age of *M. littoralis* was greater in 2006 than in 2005, as evidenced

by a significant difference in the adjusted group means (ANCOVA, $p = 0.010$, Figure 3, Table 1).

Growth rates of *M. americanus* in 2005 and *M. littoralis* in 2006 were not significantly different between seasons. However, size-at-age of *M. americanus* collected in the spring of 2005 was smaller than that for specimens collected in the summer and fall, as indicated by the significant difference in the adjusted group means (ANCOVA, $p < 0.001$, Figure 4A, Table 1). A significant difference in the adjusted group means (ANCOVA, $p < 0.001$, Figure 4B, Table 1) for *M. littoralis* collected during the 3 seasons in 2006 suggested that size-at-age in the spring was smaller than that for specimens collected in the summer and fall. For both seasonal comparisons, growth during summer and fall was similar, as shown by similar adjusted means (ANCOVA, $p > 0.05$). It should be noted that the sample size for *M. littoralis* col-

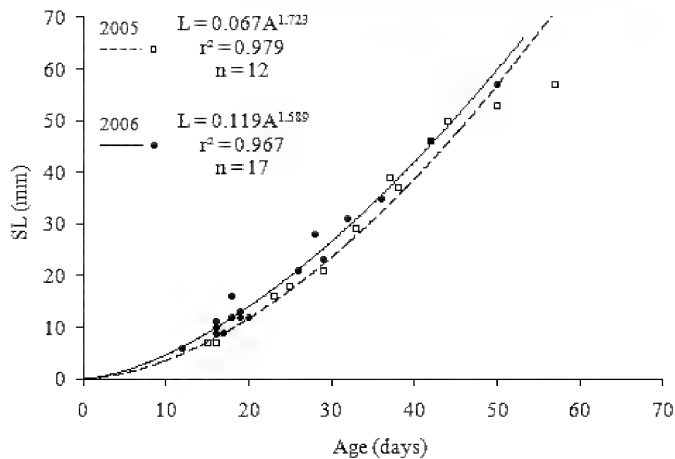


Figure 3. Relationships between age and standard length (SL) for *Menticirrhus littoralis* collected in 2005 and 2006 as represented by fitted power curves.

lected in the fall was small with only 8 otoliths available.

Menticirrhus americanus collected from mainland marsh edges grew significantly faster than *M. americanus* collected from mainland sandy shorelines in 2005 (Figures 5, Tables 1 and 2; GT2—Method comparison of slopes, $p < 0.05$). Comparison of growth for *M. americanus* collected from mainland locations and offshore surf zone habitats could not be made because relatively few *M. americanus* were collected from surf zones. In 2006 there was no significant difference in the growth rates (regression slope) of *M. americanus* collected from mainland marsh edges and sandy shorelines (Table 1). There was, however, a significant difference in adjusted group means (ANCOVA, $p = 0.05$) between *M. americanus* collected from these two mainland habitats, indicating that specimens collected in 2006 from marsh edges were of a larger size—at-age than specimens collected from sandy shorelines.

DISCUSSION

Otolith age-length relationships of kingfish indicated increased rate of growth with increasing size and warmer water temperatures. Growth rates of all 3 kingfish species were similar, ranging from about 0.7 mm/day at 4–6 mm SL to 1.9 mm/day at 55–60 mm SL. These growth rates are similar to values reported by Miller et al. (2002). Their tagging study of *M. saxatilis* found growth varied from 0.7–2.8 mm/day (among specimens 34–194 mm SL). Specimens used in this study were smaller (< 61 mm SL), which probably explains the slower maximum growth rates (< 1.9 mm/day). *Menticirrhus americanus* had similar growth in 2005 and 2006; however, size-at-age of *M. littoralis* was greater in 2006 than 2005. Water temperatures were higher in 2006 than in 2005, which may have contributed to the increased growth. Comyns et al. (1989) also reported a positive relationship between water temperature and growth for another sciaenid, *S. ocellatus*.

Growth of *M. americanus* and *M. littoralis* collected during the spring was slower than growth of fishes collected during the summer and fall. The few *M. saxatilis* that were collected during summer also grew noticeably faster than those collected in the spring. Nixon and Jones (1997) reported faster growth of young Atlantic croaker, *M. undulatus*, collected from estuarine waters of Virginia during the summer versus those collected in the fall. They concluded warmer water temperatures and higher food availability in the summer accounted for the more rapid growth. During the current study, water temperatures were similar during the spring and fall and warmest during the summer. Larger juvenile kingfish collected in the early fall may be relatively large for their age because they grew rapidly as larvae during the late summer when water temperatures were warm. In contrast, larger juvenile kingfish collected in the early spring may be small for their age because they grew slowly as larvae during the late winter when water temperatures were cooler.

Menticirrhus americanus collected in 2005 from mainland marsh edges had higher growth rates than *M. americanus* collected along mainland sandy shorelines. *Menticirrhus americanus* may have grown faster along marsh edges because pre-

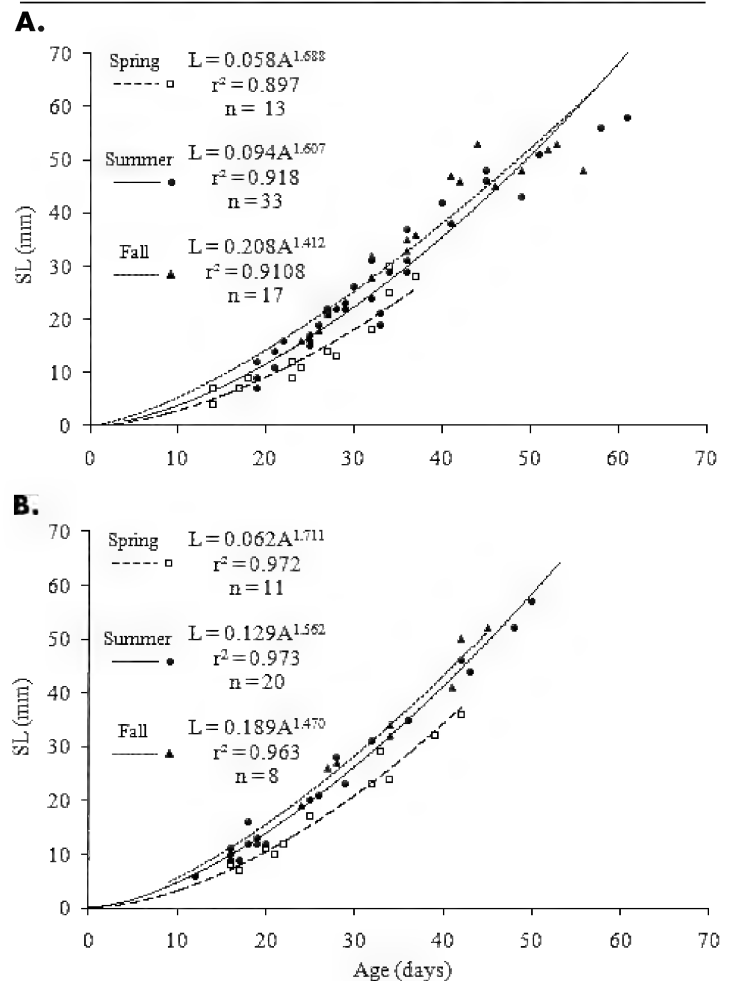


Figure 4. Relationships between age and standard length (SL) for *Menticirrhus americanus* collected during spring, summer, and fall as represented by fitted power curves. **A.** Year 2005. **B.** Year 2006.

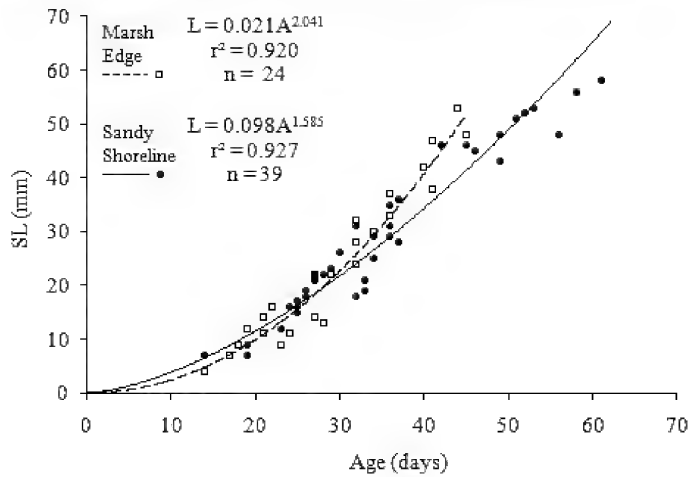


Figure 5. Relationships between age and standard length (SL) for *Menticirrhus americanus* collected from the mainland marsh-edges and sandy shorelines in 2005 as represented by fitted power curves.

dation pressure was less within the emergent vegetation or because the probability of foraging success was higher. Several studies have compared growth rates of juvenile fish collected from vegetated and nonvegetated habitats. Sogard et al. (1992) held juveniles of 3 species (*Pseudopleuronectes americanus*, *Tautoga onitis*, and *Gobiosoma bosc*) in cages in areas with submerged vegetation and in nonvegetated areas and found that only *T. onitis* showed faster growth with the presence of vegetation. *Tautoga onitis* showed a clear preference for vegetated habitats, as none were collected from throw trap samples from nonvegetated habitats. *Pseudopleuronectes americanus* and *G. bosc* were abundant in both types of habitats, but faster growth rates occurred within the nonvegetated habitats. Levin et al. (1997) reported that *Lagodon rhomboides* from artificial grass bottoms grew significantly faster than those from nonvegetated sand bottoms. They concluded that *L. rhomboides* may select vegetated habitats because high growth rates could lead to lower mortality. Using enclosures, Stunz et al. (2002) determined that growth rates of juvenile *S. ocellatus* were higher in salt marsh and seagrass vegetation than over nonvegetated bottoms and oyster reefs. Using otoliths, they also showed that free-living *S. ocellatus* collected from salt marsh, seagrass, and nonvegetated bottoms had similar growth rates, which they attributed to movement among habitats. Another study by Zapfe and Rakocinski (2008) compared growth of young *L. xanthurus* (20–60 mm SL) during marsh access and marsh restriction in coastal Mississippi. In contrast to this study, they found growth of *L. xanthurus* decreased with access to emergent shoreline vegetation (ESV) and increased with less access to ESV. This may be due to differences in prey selection considering juvenile *L. xanthurus* feed mostly on polychaetes by

sifting through the bottom sediment (Zapfe and Rakocinski 2008), whereas kingfish collected from the marsh edge fed preferentially on mysids (Anderson 2009).

Other studies from freshwater systems have compared growth rates of juvenile fish, and documented the effects of habitat structural complexity and other interactions on fish growth. Crowder and Cooper (1982) compared the diets of *Lepomis macrochirus*, collected from experimental ponds with varying vegetation and reported that fish grew better in ponds with intermediate vegetation densities than in those with low and high vegetation densities. They concluded that several variables including food, habitat structure, temperature and predators influenced fish growth along with behavioral changes of both prey and predator. Werner and Hall (1988) reported that *L. macrochirus* ontogenetically shifted habitats in response to feeding rate and predation risk. They also determined that if predator densities increased, *L. macrochirus* delayed shifting habitats to avoid predation. *Menticirrhus americanus*, which were most abundant from mainland sandy shoreline, were also numerous along marsh edges (Anderson 2009). Movement of *M. americanus* between these habitats was unlikely, as growth of similar-sized *M. americanus* from marsh edge was faster than growth of fish from sandy shorelines. Shervette and Gelwick (2007) used enclosures to determine relative growth rates of juvenile *L. rhomboides* in marsh edge, oyster, and nonvegetated habitats. They found highest growth rates from the marsh edge habitat and lowest growth rates from the nonvegetated habitat.

This research shows that both abiotic and biotic factors can affect the growth of young kingfish. Increased growth was associated with specimens collected from warmer water temperatures (during the summer and fall) and also those from marsh edge habitat. Many studies have documented that a combination of factors influence the growth of young fish. Rakocinski et al. (2006) showed that fluctuations in growth of juvenile *L. xanthurus* were tied to short term changes in water temperature and salinity. Baltz et al. (1998) determined that water temperature, salinity, and dissolved oxygen contributed more to growth of juvenile *C. nebulosus* and *S. ocellatus* than diet or grass stem density. Although they did not compare growth of fish from different habitats, they did show that a combination of abiotic and biotic factors contributed to fish growth. Growth comparison studies of young fish from different habitats aid in understanding the early

TABLE 2. Comparison intervals (95%) of regression coefficients of the growth rate (slope) for *Menticirrhus americanus* collected from marsh-edge and sandy shoreline habitats. Comparison intervals were computed via the GT2-method (Sokal and Rohlf 1995). Sample sizes are presented along with the confidence interval ranges.

Species	Habitat	Sample size	Slope	Comparison interval range
<i>M. americanus</i>	Marsh edge	24	2.041	(1.864 – 2.220)
<i>M. americanus</i>	Sandy shoreline	39	1.585	(1.454 – 1.719)

life history of estuarine—dependant fish. Also, research that documents the importance of marsh edge habitat is particularly relevant in the northcentral GOM because this region

has seen tremendous population growth and development during the past decade, and shoreline habitats continue to be degraded by anthropogenic influences.

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Flexible Feeding Strategies of Juvenile Gray Triggerfish (*Balistes capriscus*) and Planehead Filefish (*Stephanolepis hispidus*) Within Sargassum Habitat

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FLEXIBLE FEEDING STRATEGIES OF JUVENILE GRAY TRIGGERFISH (*BALISTES CAPRISCUS*) AND PLANEHEAD FILEFISH (*STEPHANOLEPIS HISPIDUS*) WITHIN *SARGASSUM* HABITAT

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ABSTRACT: *Sargassum*—associated juvenile gray triggerfish and planehead filefish exhibited flexible feeding strategies in terms of their use of epifauna or pelagic zooplankton. Four diet samples represented instances of co—occurrence and segregated occurrence. Co—occurring gray triggerfish had the most specialized diets consisting mainly of pelagic copepods and hyperiid amphipods. Conversely, segregated triggerfish as well as both co—occurring and segregated filefish had broader diets mainly consisting of *Sargassum* epifauna, such as bryozoans, portunid crabs, and hippolytid shrimp. Still, co—occurring planehead filefish also consumed somewhat more zooplankton than segregated planehead filefish. Ontogenetic diet transitions were not as distinct for gray triggerfish as for planehead filefish. Our study demonstrates that juvenile tetradonts can be flexible in their use of benthic versus pelagic feeding strategies. Consequently, the influence of these key consumers on *Sargassum* food webs may vary spatiotemporally.

KEYWORDS: fish feeding strategies, gray triggerfish, planehead filefish, *Sargassum*, Tetraodontiformes

INTRODUCTION

Brown macroalgae in the genus *Sargassum* forms extensive free—floating mats of structured habitat in surface waters of the Gulf of Mexico (GOM) and the Atlantic Ocean. *Sargassum* has recently been designated as Essential Fish Habitat (EFH) by the South Atlantic Fisheries Management Council (SAFMC 2002 in Casazza 2008). Functionally, the *Sargassum* complex provides potential refuge, feeding and spawning habitat for various pelagic fishes (Dooley 1972, Bortone et al. 1977, Kingsford and Choat 1985, Kingsford 1992, 1993, Druce and Kingsford 1995, Moser et al. 1998, Wells and Rooker 2004). As a mobile habitat, *Sargassum* also provides a vehicle of transport and dispersal for juvenile fishes and other organisms (Casazza 2008).

A growing awareness of the ecological importance of *Sargassum* has motivated recent studies of its role as a unique nursery habitat in the northwestern GOM (Rooker et al. 2004, 2006, Wells and Rooker 2004, Turner and Rooker 2006), the north-central GOM (Comyns et al. 2002), and the northwestern Atlantic (Casazza 2008, Casazza and Ross 2008). Although few organisms directly consume *Sargassum* (Rooker et al. 2006), the *Sargassum* complex consists of a diverse trophic network of epifaunal and epiphytic constituents (Coston—Clements et al. 1991). Marine rafting fauna represent all major trophic categories, including suspension—feeding, grazing, and boring organisms (Thiel and Gutow 2005). Pelagic—derived zooplankton also concentrate near *Sargassum* (Yeatman 1962), thus enhancing the pelagic feeding option for *Sargassum* occupants.

Juvenile gray triggerfish (*Balistes capriscus*) and planehead filefish (*Stephanolepis hispidus*) represent two of the most abundant fishes associated with *Sargassum* (Dooley 1972, Bortone et al. 1977, Coston—Clements et al. 1991, Settle 1993, Casa-

zza and Ross 2008). Planehead filefish usually ranks as the most abundant member of the *Sargassum* ichthyofauna, and gray triggerfish typically ranks among the top 3 most abundant fishes associated with *Sargassum*. Although there is some seasonal non—overlap, juveniles of both species often co—occur in association with *Sargassum* (Dooley 1972). As tetradonts, the body design of these fishes exemplifies agile maneuverability enabled by independently undulating paired and median fins (Arreola and Westneat 1996). This derived body design combined with a nimble but strong oral—jaw apparatus and dentition also promotes feeding plasticity (Kotrschal 1989, Turingan 1994, Vose and Nelson 1994).

Previous studies have noted that diets of juveniles of both fishes contain *Sargassum* associated epifauna as well as pelagic zooplankton (Dooley 1972, Coston—Clements et al. 1991, Harper and McClellan 1997, Turner and Rooker 2006, Casazza 2008). However, previous studies have not considered whether such diet breadth might represent flexible feeding strategies. The overall goal of this study was to compare the diets of *Sargassum*—associated juvenile planehead filefish and gray triggerfish to assess feeding flexibility among the limited set of ecological circumstances. Four population samples represented instances of co—occurrence and segregated occurrence for these fishes. Diet patterns were examined in terms of (1) the relative use of pelagic versus *Sargassum*—associated prey, (2) diet breadth and (3) diet dissimilarity. We hypothesized that variability in diets of these 4 populations of tetradonts reflect flexibility in feeding strategies relative to *Sargassum* versus nearby open water as sources of food. As a caveat, the limited set of diet samples was not robust enough for generalizing about co—occurring versus segregated settings or seasonal diet patterns.

MATERIALS AND METHODS

Sample collections

Four population samples of planehead filefish or gray triggerfish taken in association with *Sargassum* and representing different ecological settings were used for this study. A sample containing 74 planehead filefish was collected on 21 May 2000 from patchy *Sargassum* habitat at 29°32.54'N and 87°02.81'W. Samples of 69 planehead filefish and 55 gray triggerfish were collected on 15 October 2000 from a *Sargassum* mat at 28°44.82'N and 87°42.28'W. Another sample containing 70 gray triggerfish was collected on 10 July 2002 from patchy *Sargassum* habitat at 29°02.29'N and 88°48.68'W.

Sightings of *Sargassum* by small aircraft pilots directed the R/V *Tommy Munro* to sampling sites. Upon arrival, surface collections were taken by towing a neuston plankton net (4 m long x 2 m wide x 1 m high, 3.22 mm nitex mesh) directly through weed lines, mats, or clumps to sample *Sargassum* along with associated epifauna and fishes. Accompanying hydrographic measurements included water clarity (Secchi), water temperature (°C), surface salinity and dissolved oxygen (mg/l). Time of day, cloud cover, sea state, sample depth, water depth, wind speed and direction, and latitude and longitude were also recorded for each collection site.

Net caught *Sargassum* was placed on fixed wire mesh suspended ~70 mm above the bottom of a 2.5 m long fiberglass trough situated above a wash table. *Sargassum* samples were irrigated with seawater to wash associated organisms through a hole in the wash table and into a 0.505 mm mesh cone which retained the organisms. Organisms were fixed in 95% ethanol and labeled. Collections that were too large to preserve in entirety were subsampled by removing up to 50 kg wet weight of *Sargassum*. The remaining *Sargassum* along with associated organisms was then weighed and discarded.

Laboratory procedures

Diet Analysis. In the laboratory, fishes were removed from *Sargassum* samples and identified. Associated invertebrates were also retained and stored in ethanol. Each fish specimen was kept individually in 95% ethanol and assigned a unique number. For each specimen, total length (TL), standard length (SL), mouth width, head length, and body depth were measured to the nearest 0.01 mm using dial calipers. Blotted and gutted wet weights were taken for each fish to the nearest 0.01 g using an Ohaus® Analytical Plus microbalance.

For diet analysis, food items were recovered from the mouth cavity, gills, and complete digestive tract and preserved in 70% ethanol in labeled vials. First, guts were removed by making a ventral incision along the fish from the anus towards the operculum. The entire digestive tract from the esophagus to anus was removed and placed in a dish, incised and teased apart to remove any food items, and irrigated to remove any remaining food items.

All food items were identified to the lowest practical taxonomic level, usually family. For each fish, the volume of each type of food item was determined using a modified squash plate technique (Hellawell and Abel 1971), following Rakocinski and Zapfe (2005).

Volumes of diet taxon fractions were estimated using a Nikon image analysis system consisting of a DMX 1200 Digital camera attached to a SMZ 1500 stereomicroscope and a PC. Using MetaVue 5.0 imaging software, prey volumes were estimated from two dimensional areas compressed to a uniform thickness between calibrated squash plates (Hellawell and Abel 1971). Multiple organisms were arranged to minimize the amount of unfilled space between them to ensure accurate volume estimates. Excess liquid was soaked up using a tissue before squashing. A digital picture was taken of the compressed area at a known magnification. Digital outlines of squashed diet fractions were traced twice to within a 0.1 mm² area tolerance in MetaVue 5.0 (Rakocinski and Zapfe 2005). Conversion factors specific to the calibrated squash plates facilitated volume (μL) estimations from mean areas (mm²). Volumes were recorded along with numbers of items for each prey type per fish.

Epifaunal Prey Abundances. Abundances and sizes (i.e., volumes) of epifaunal organisms were quantified as potential prey from *Sargassum* samples used for diet studies. First, *Sargassum* along with associated epifauna were subsampled into equal homogeneous fractions using a Motodo plankton splitter (Motodo 1959). One-fourth of the original sample was used for the segregated gray triggerfish and the co-occurrence sample; and a 1/8 fraction was used for the segregated planehead filefish sample. After removing all *Sargassum* fragments from retained fractions, the sorted organisms were split twice more, leaving 1/16 of the original epifauna for the segregated gray triggerfish and co-occurrence samples, and 1/32 of the original epifauna for the segregated planehead filefish sample. Organisms from the subsamples were identified and counted. Volumes for each taxonomic group were determined using the modified squash plate procedure as described above. Organisms that were too large for the squash plate procedure were placed in a drying oven for 48 hours at about 65°C before weighing them to the nearest 0.01 g (Hyslop 1980). Organisms from *Sargassum* samples retained by a 5.6 mm sieve were not regarded as potential prey due to gape size limitations of the fishes examined.

Data analysis

Diet Composition. Diets of 143 planehead filefish and 125 gray triggerfish were examined for this study. Basic diet metrics for each fish included counts and volumes for each prey type and frequency of occurrences (FO) for each fish sample. Diet analyses were mainly based on prey volumes to obviate biases associated with using counts for diet studies (e.g., 1 large prey versus equal volume made up of many small prey) and the problem of being unable to assign counts to some important prey types (e.g., colonial bryozoans and hydroids). Moreover, to avoid sacrificial pseudo-replication (Wallace 1981, Krebs 1999), diet proportions were calculated for each individual fish before averaging across the entire diet sample (VanderKooy et al. 2000). To consider ontogenetic diet shifts, fishes were subdivided into three natural size groupings (small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL)). Lengths ranged from 9.8 mm to 71.2 mm SL for gray triggerfish and

from 19.1 mm to 71.2 mm SL for planehead filefish, although large fish were generally less than 50 mm SL. To ensure that the sample sizes (i.e., $n = 56 - 74$) of fishes adequately represented population-level diets and to estimate diet richness, the cumulative number of prey taxa was plotted against the number of pooled stomachs. Smoothed species-area curves representing every possible sequence of fish specimens within samples were generated, following Hartnoll (1983).

Consumption of *Sargassum* Epifauna versus Zooplankton. The extent to which fishes consumed *Sargassum*-associated epifauna or zooplankton was examined for each species-size group. Epifaunal and zooplankton groupings were assigned to food items based on the literature (Morris and Mogelberg 1973, Coston-Clements et al. 1991, Smith and Johnson 1996). For each fish, epifauna and zooplankton volumes were normalized by the total amount of food in the diet, and resulting proportional values were arcsine square root transformed. Gut fullness (i.e., total prey mass/fish mass) was also compared among size class groups.

Diet Breadth. Diet breadth based on prey volume was calculated using Levins' Index (B) and then standardized so it was expressed on a scale from 0 to 1.0, following Krebs (1999). The proportion of items in the diet (p_j) represented by each of food category j was estimated by N_j/Y , where N_j = number of individuals in j and $Y = \sum N_j$ (i.e., total number of individuals sampled).

Levins' Index was calculated as:

$$B = 1/\sum p_j^2.$$

Levins' B ranges from 1 to n , where n is the total number of prey types. To make interpretation easier, the values were standardized by dividing the total number of prey types into B , after correcting for a finite number of prey types (Krebs 1999):

$$B_A = (B - 1)/(n - 1);$$

where B_A = Levins' standardized niche breadth, B = Levins' index of niche breadth, and n = number of possible resource states (i.e., prey types). After standardization, 0 signifies a minimum niche breadth and extreme specialization, whereas 1.0 signifies maximum niche breadth and extreme generalization. Levins' Index of diet breadth was calculated both for each fish sample as whole, and separately for each size class within samples.

Diet Ordination. Diet similarity patterns were examined using non-metric Multi-Dimensional Scaling (NMDS) in Primer ver. 6.0. Percent volumes for prey types were square root transformed before conversion into a resemblance matrix of Bray-Curtis similarity values, which were subsequently subjected to NMDS ordination. The Bray-Curtis similarity coefficient is considered the most appropriate index for comparing biological communities (Clarke and Gorley 2006). Similarity values range from 0 to 100, with 100 signifying perfect similarity. Coordinates in NMDS plots represented diets of individual fish in 2 dimensional NMDS space, and distances between coordinates reflected diet dissimilarity.

ANOSIM and SIMPER Analyses. Analysis of Similarity (ANO-

SIM) followed by the Similarity Percentages Routine (SIMPER) elucidated overall differences in the diet composition of fishes. ANOSIM tests in Primer ver. 6.0 compared diets among samples and size classes of planehead filefish and gray triggerfish. The ANOSIM permutation test statistic, R , is centered on 0 (no differences among the groups). As R approaches 1, the null hypothesis is rejected indicating a significant difference among groups (Clarke and Gorley 2006).

SIMPER in Primer ver. 6.0 was used to attribute dietary differences to particular prey types when ANOSIM tests were significant (Clarke and Gorley 2006). SIMPER breaks down the average Bray-Curtis dissimilarity into percentage contributions from each prey type, thus showing which prey types primarily contributed to dietary differences. An overall two-way SIMPER analysis compared diet dissimilarity between gray triggerfish and planehead filefish as well as between segregated and co-occurring size-classes. In addition, one-way SIMPER tests elucidated diet dissimilarity between size classes.

RESULTS

Diet overview

A total of 32 prey types were recognized among all 4 samples. Predominant epifaunal prey types included bryozoans, hydroids, hippolytid shrimp, portunid crabs, caprellid amphipods, nereid polychaetes, triphorid gastropods, serpulid polychaetes, and phoxichilid sea spiders. Important pelagic prey types included calanoid copepods, cyclopoid copepods, corycaeid copepods, hyperiid amphipods, and fish eggs. Partially digested food was generally categorized as unidentified (unid) shrimp, unid brachyuran, unid copepod, unid gastropod, or unid miscellaneous material. Guts of 4 of the 74 segregated planehead filefish (5.4%; $n = 70$) were empty; as well as 1 of the 69 co-occurring planehead filefish (1.4%; $n = 68$); 0 of the 55 co-occurring gray triggerfish (0%; $n = 55$), and 3 of the 70 segregated gray triggerfish (4.3%; $n = 67$).

Smoothed species-area curves indicated that the sample sizes were sufficient, and thus provided comparable estimates of diet richness (Figure 1). The segregated gray triggerfish sample exhibited the highest diet richness, as signified by a curve that leveled out at about 25 prey types. In contrast, co-occurring gray triggerfish exhibited the lowest diet richness of about 14 prey types. Curves for both segregated and co-occurring planehead filefish reached similar values of around 20 and 22 prey types, respectively. However, the curve for co-occurring planehead filefish began to level off prior to that for the segregated filefish, reflecting fewer infrequent prey types in the co-occurring sample.

Epifaunal prey abundance and gut fullness

Prey abundances were quantified as standardized volumes (ml/kg) of epifaunal prey taxa, except organisms retained by a 5.6 mm sieve that were excluded from consideration. This criterion excluded mostly larger portunid crabs and palaemonid shrimp. Consequently, the total volume of potential epifaunal prey was highest for the segregated planehead filefish *Sargassum* sample (1144.6 ml/kg; included prey = 15.6 % of total volume); followed by the co-occurring *Sargassum* sample

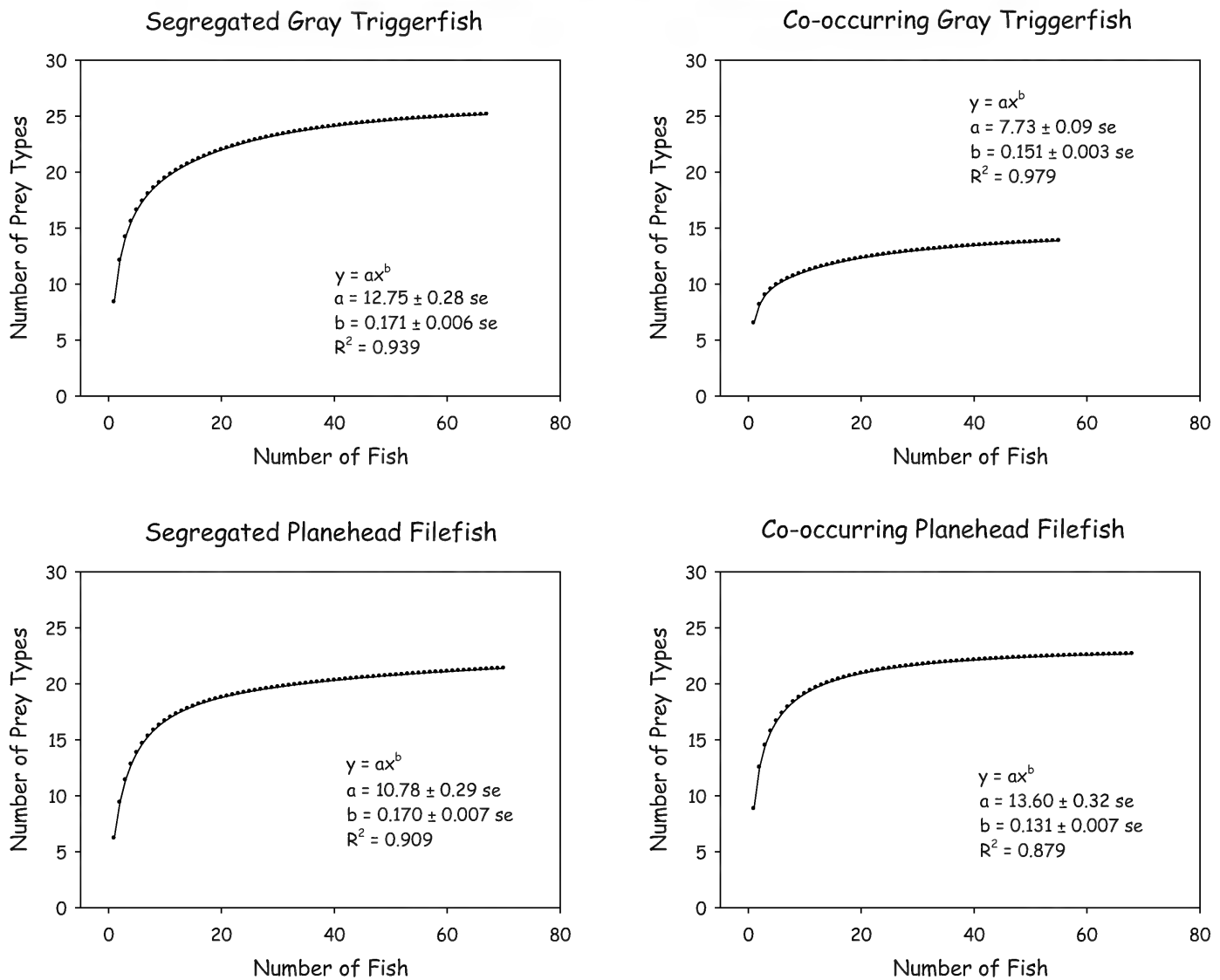


Figure 1. Smoothed species–area curves for segregated gray triggerfish, segregated planehead filefish, and for co-occurring gray triggerfish and planehead filefish samples.

(915.4 ml/kg; included prey = 84.9 % of total volume), and by the segregated gray triggerfish *Sargassum* sample (712.4 ml/kg; included prey = 71.3 % of total volume). Relative abundances of smaller, more vulnerable potential prey were highest for the co-occurring *Sargassum* sample, as implied by the relatively steep slope and high intercept of the normalized biomass–size spectrum (NBSS) (slope = -1.07 , intercept = 4.78 ; $r^2 = 0.73$, $n = 8$ for co-occurring species vs. slope = -0.701 , intercept = 3.78 , $r^2 = 0.59$, $n = 8$ for segregated triggerfish and slope = -0.44 , intercept = 3.07 , $r^2 = 0.58$, $n = 10$ for segregated filefish).

Together, hippolytid, palaemonid, and unidentified shrimp, in addition to serpulids and planocerids (planocercid flatworms) made up over 90% of the total biomass of recovered potential epifaunal prey in the segregated triggerfish *Sargassum* sample. Hippolytid shrimp was the most prevalent prey item within the segregated filefish *Sargassum* sample, making up almost 80% of the potential prey biomass. Palaemonid and unidentified shrimp

made up an additional 10% of the biomass of potential prey in this sample. Relative prey proportions for the co-occurrence *Sargassum* sample were very similar to those for the two segregated samples. Hippolytid shrimp alone made up 91% of the potential prey biomass for the former sample. Together, palaemonid and unidentified shrimp also contributed an additional 4.7% of the potential prey biomass for this *Sargassum* sample.

Segregated gray triggerfish showed the lowest gut fullness, and segregated planehead filefish showed somewhat lower gut fullness than co-occurring fishes (Figure 2). Co-occurring fishes of both species contained relatively similar amounts of food in their guts. There was no consistent pattern among size classes in the relative amounts of food in the guts, although medium sized fish contained slightly more food than large and small fish, especially within segregated samples.

Feeding strategies

Dependence on benthic or pelagic feeding strategies varied

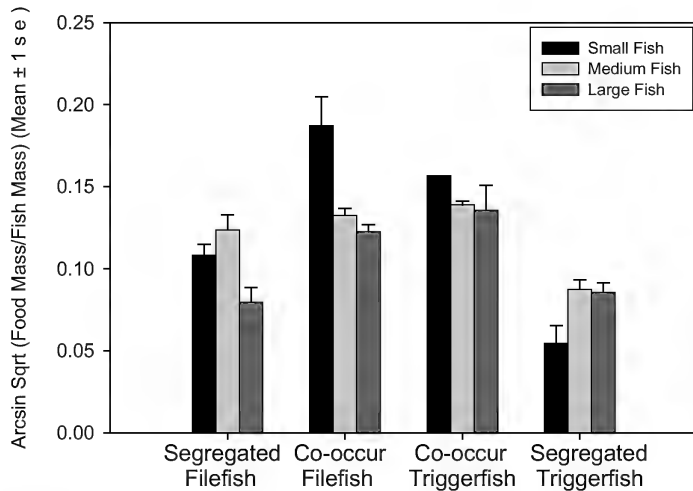


Figure 2. Relative gut fullness (mean \pm se) for 3 size classes of segregated and co-occurring samples of planehead filefish and gray triggerfish. Lack of error bar reflects small n for small co-occurring triggerfish. Size classes represent small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL) fishes.

among the 4 samples of tetraodontids. Overall, co-occurring gray triggerfish consumed the highest relative amounts of zooplankton; whereas segregated triggerfish consumed the highest relative amounts of epifaunal prey (Figure 3). Both co-occurring and segregated planehead filefish consumed relatively high amounts of epifaunal prey. However, co-occurring planehead filefish consumed somewhat greater relative amounts of zooplankton than segregated filefish. Large co-occurring planehead filefish relied much more heavily on epifaunal sources of food than either small or medium fish; however, this was not the case for segregated filefish.

Diet Breadth. Overall, co-occurring gray triggerfish displayed the narrowest diets whereas co-occurring planehead filefish had the broadest diets (Table 1). Segregated gray triggerfish also had much broader diets than co-occurring triggerfish. Conversely, segregated planehead filefish had somewhat narrower diets than co-occurring filefish. Surprisingly, large size classes typically had narrower diets than small or medium size classes.

NMDS Ordination. NMDS plots depicted diet similarity patterns for samples of planehead filefish and gray triggerfish (Figure 4). A stress value of 0.18 indicated that diet variation was fairly well represented by the first two NMDS dimensions. Segregated planehead filefish and gray triggerfish occupied much broader regions of NMDS space than their co-occurring counterparts; coordinates of co-occurring individuals were relatively aggregated within NMDS space. Co-occurring gray triggerfish occupied the narrowest and most exclusive diet-ordination space. In contrast, co-occurring planehead filefish characterized a much broader region of ordination space. However, segregated planehead filefish occupied the most extensive region of NMDS space.

Ontogenetic diet transitions were also apparent within NMDS ordination space (Figure 4). Generally, size classes of planehead filefish were discernible as dispersion patterns within ordination space. Size classes of the co-occurring planehead

filefish were more discernable than those of the segregated planehead filefish. Conversely, ontogenetic diet transitions were not as apparent for gray triggerfish. For example, size classes of segregated gray triggerfish were not sharply delineated in NMDS space, even though they occupied a fairly broad region of ordination space. In contrast, all 3 size classes of co-occurring gray triggerfish clustered within a narrow region of NMDS diet-ordination space.

ANOSIM and SIMPER. ANOSIM showed that diet composition strongly differed between co-occurring and segregated gray triggerfish (ANOSIM $R = 0.817$; $p < 0.001$) and SIMPER confirmed the marked difference in diet composition (average dissimilarity = 89.69%) and illustrated how it was expressed. Consumption of pelagic calanoid copepods (74.27% vs. 2.94% volume) and hyperiid amphipods (8.39% vs. 0.26% volume) accounted for much of the diet dissimilarity between these samples. Segregated gray triggerfish mainly consumed large epifaunal prey, including bryozoans (17.50% volume), portu-

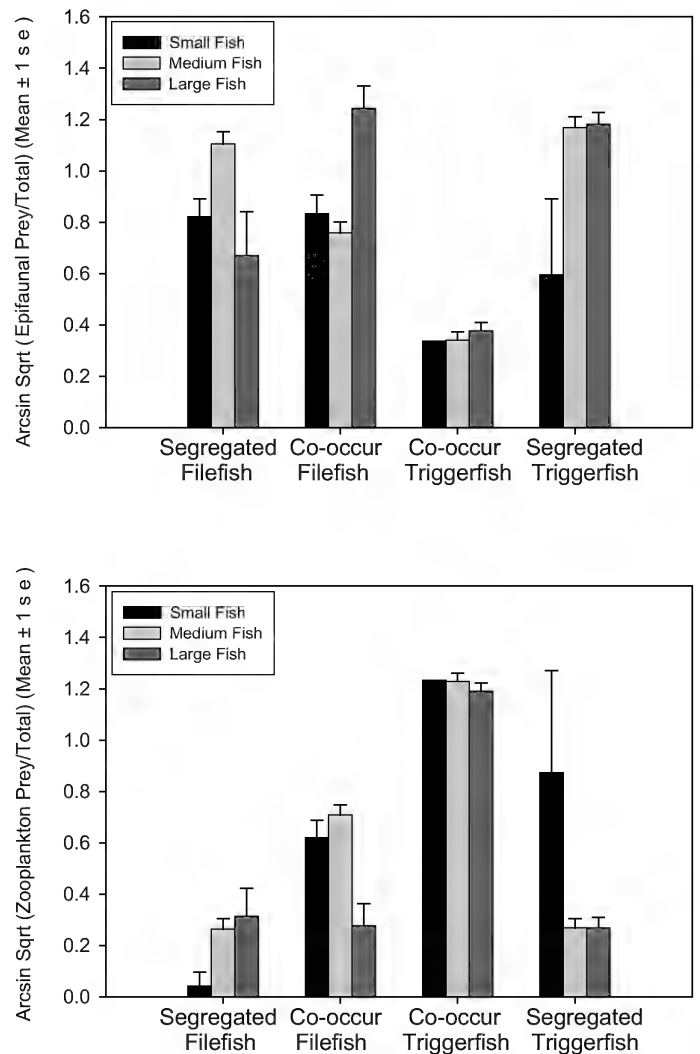


Figure 3. Relative amounts (mean \pm se) of epifaunal (top panel) and zooplankton (bottom panel) prey for 3 size classes of planehead filefish and gray triggerfish within segregated and co-occurring samples. Lack of error bars reflects small n for small co-occurring triggerfish. Size class definitions described in legend for Figure 2.

TABLE 1. Levins's diet breadth (B) and standardized Levins's diet breadth (B_A) for tetraodontid diet samples. Standardized diet breadth values (B_A) show that large fishes consistently exhibited the most specialized diets. Size classes represent small (< 20 mm SL), medium (20–30 mm SL), and large (> 30 mm SL) fishes

		Levins' Measure (B)	Standardized Levins' Measure (B_A)
Segregated Gray Triggerfish	Overall	10.6980	0.3879
	Small	5.0546	0.5068
	Medium	10.3995	0.4087
	Large	8.5564	0.3149
Co-occurring Planehead Filefish	Overall	10.0811	0.4128
	Small	6.8720	0.3091
	Medium	9.3272	0.3785
	Large	3.7693	0.1539
Co-occurring Gray Triggerfish	Overall	1.7660	0.0547
	Small	1.5692	0.0712
	Medium	1.7666	0.0639
	Large	1.7746	0.0596
Segregated Planehead Filefish	Overall	8.1687	0.3258
	Small	7.8354	0.3598
	Medium	7.8223	0.3790
	Large	4.1705	0.2114

nid crabs (13.79% volume), and hippolytid shrimp (12.41% volume).

Diet dissimilarity was also significant between co-occurring and segregated planehead filefish (ANOSIM $R = 0.376$; $p < 0.001$), as illustrated by moderately high SIMPER dissimilarity (average dissimilarity = 78.65%). Although bryozoans comprised roughly similar diet proportions in both samples of filefish (10.91% vs. 9.14% volume); co-occurring filefish consumed more planktonic calanoid copepods (16.41% vs. 7.14% volume), in addition to certain epifaunal prey, including hippolytid shrimp (15.53% vs. 2.89% volume), and triphorid gastropods (10.08% vs. 0.08% volume). Diets of segregated planehead filefish contained notably more unidentified miscellaneous material (24.79% vs. 7.90% volume) and hydroids (16.51% vs. 3.58% volume) than co-occurring filefish.

Although co-occurring gray triggerfish and planehead filefish were collected from the same *Sargassum* habitat, ANOSIM revealed significant diet dissimilarity between these population samples (ANOSIM $R = 0.463$; $p < 0.001$). SIMPER corroborated fairly high diet dissimilarity between these co-occurring fishes (average dissimilarity = 66.82%). Calanoid copepods mainly contributed to the difference in diets between the two co-occurring species; calanoids were much more prevalent in the diet of gray triggerfish (74.27% vs. 16.41% volume). Another zooplankton prey type, hyperiid amphipods, was almost equally represented in the diets of both fishes (8.39% triggerfish vs. 7.48% filefish volume). However, diets of co-occurring filefish also contained much higher amounts of several epifaunal prey, including hippolytid shrimp (15.53% vs. 0.11% volume), bryozoans (10.91% vs. 0% volume), and triphorid gastropods

(10.08% vs. 1.77% volume).

Diets of the size classes of co-occurring gray triggerfish were least distinct compared to other samples (average SIMPER dissimilarity = 27.71% – 32.48%). There were too few small fish ($n = 1$) to warrant reliable comparisons with this size class. However, the diets of medium and large size classes of co-occurring gray triggerfish were significantly different (ANOSIM $R = 0.212$; $p = 0.001$). Calanoid copepods largely contributed to size-related diet dissimilarity involving large fish (i.e., 7.50% SIMPER dissimilarity with medium fish); notwithstanding similar and high calanoid percent volumes for all three size classes (74.06% – 79.12%). In addition, the use of certain large prey, including unidentified shrimp, increased with fish size.

Pairwise ANOSIM showed a moderate difference in diet similarity between medium and large size classes of segregated gray triggerfish ($R = 0.068$; $p = 0.014$). There were too few small fish ($n = 2$) to warrant reliable comparisons with this size class. Diet dissimilarity between medium and large fish was mainly attributable to greater consumption of portunid crabs (10.19% dissimilarity), bryozoans (6.82% dissimilarity), and hippolytid shrimp (6.53% dissimilarity) by large fish. Diets of medium segregated gray triggerfish were further distinguished by the use of hydroids (9.42 % volume), and ostracods (10.62 % volume).

Diets differed significantly among all 3 size classes of co-occurring planehead filefish (ANOSIM $R = 0.322$ – 0.601 ; all $p = 0.001$); as further illustrated by SIMPER (average dissimilarity = 58.12% – 79.22%). Although small crustaceans, such as calanoid copepods and ostracods, contributed markedly to size-related diet dissimilarities (e.g., combined = 45.46% vs. 6.48% volume for small vs. large fish), other large epifauna, including hippolytid shrimp, as well as bryozoans, also contributed noticeably to size-related dietary differences (e.g., combined = 5.00% vs. 69.57% volume for small vs. large fish). Accordingly, hippolytid shrimp and bryozoans together made up 41.1% of the diet dissimilarity between small and large co-occurring planehead filefish.

SIMPER showed that the diets of all 3 size classes of segregated planehead filefish were fairly distinct (average dissimilarity = 66.23%–78.50%). The diet composition of large segregated planehead filefish differed significantly from diets of small and medium fish (ANOSIM $R = 0.321$ and 0.413 ; $p = 0.001$). Unidentified amorphous (miscellaneous) material contributed substantially to the diets of all 3 size classes of segregated planehead filefish (13.29–41.55% of volume). In addition, bryozoans mainly discriminated the diets of large segregated planehead filefish from small filefish (e.g., 3.58% vs. 21.13% volume for small vs. large fish); whereas the use of bryozoans was similar between large and medium fish (e.g., 19.92% volume for medium fish).

DISCUSSION

By virtue of their high abundances, juvenile planehead filefish and gray triggerfish likely play key roles within the food web of the *Sargassum* complex in the northern GOM. In addition to our study, previous studies have noted that diets of juveniles of both species include both *Sargassum*–associated epifauna as well

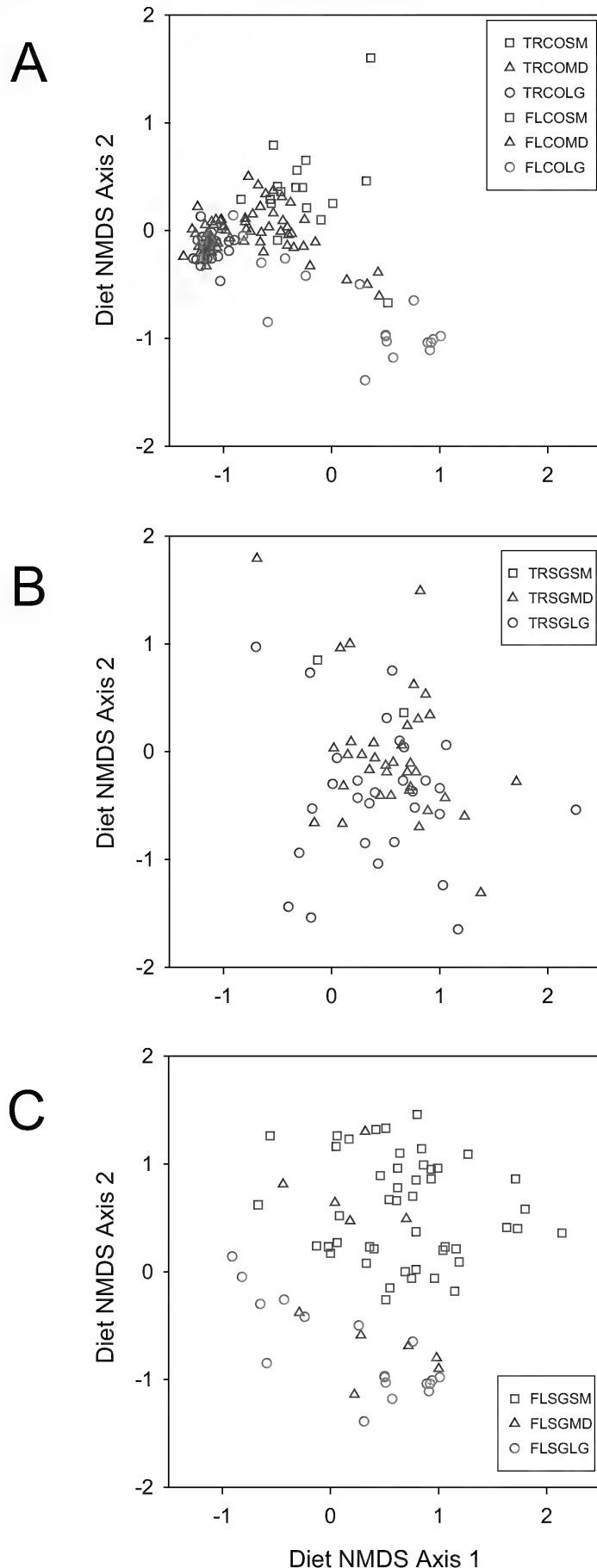


Figure 4. Non-metric multidimensional scaling (NMDS) ordination for individual fishes within the first two NMDS dimensions. **A.** Co-occurring gray triggerfish and planehead filefish coded by size class. **B.** Segregated gray triggerfish coded by size class. **C.** Segregated planehead filefish coded by size class. Size class definitions described in legend for Figure 2. Key: TRCOSM – small co-occurring triggerfish; TRCOMD – medium co-occurring triggerfish; TRCOLG – large co-occurring triggerfish; FLCOSM – small co-occurring filefish; FLCOMD – medium co-occurring filefish; FLCOLG – large co-occurring filefish; TRSGSM – small segregated triggerfish; TRSGMD – medium segregated triggerfish; TRSGLG – large segregated triggerfish; FLSGSM – small segregated filefish; FLSGMD – medium segregated filefish; FLSGLG – large segregated filefish.

as pelagic zooplankton. For example, juveniles of both species often feed on *Sargassum*-associated hydroids, bryozoans, polychaetes, and various crustaceans (Dooley 1972, Coston-Clements et al. 1991, Harper and McClellan 1997, Casazza 2008). Thus, they may rely considerably on *Sargassum*-associated secondary production as a food source. Pelagic copepods can also contribute substantially to the diet of juvenile gray triggerfish (Casazza 2008). Moreover, as seen in our study, planehead filefish also consume at least some zooplankton. But previous studies have not considered whether such diet variability might reflect flexible feeding strategies and food web impacts.

Flexible consumption of *Sargassum*-associated epifauna by juvenile tetradont fishes suggests potentially varying impacts upon the *Sargassum* food web. For example, some epifaunal prey organisms, including various small caridean shrimps and gastropods, likely graze upon epiphytic diatoms. Predation on grazing epifauna could potentially affect the condition of the *Sargassum* though cascading effects on epiphytic algae, as has been inferred for nearshore submerged vegetation (Drury-McCall and Rakocinski 2007). Conversely, suspension feeding epifauna like bryozoans and hydroids are linked to pelagic-derived production. Nevertheless, predation upon suspension feeding epifauna could also potentially enhance *Sargassum* by reducing fouling of this macroalgae.

Tetradont fishes possess derived morphological and behavioral traits that when taken together should facilitate feeding flexibility and a broad fundamental feeding niche. Notwithstanding the phylogenetic affinity between gray triggerfish and planehead filefish, they exemplified dichotomous feeding strategies in our study. When the species co-occurred in the same sample, juvenile gray triggerfish largely employed a pelagic feeding strategy on zooplankton; whereas planehead filefish mostly focused on *Sargassum*-associated epifauna. Segregated samples of both fishes largely relied on a benthic feeding strategy. Thus, our study shows that these tetradont fishes exercise flexible feeding strategies under different ecological scenarios. Previous studies have not emphasized the expression of such a flexible feeding dichotomy for these derived tetradont fishes.

Both pelagic and benthic feeding strategies may present viable options to consumers possessing suitable feeding adapta-

tions. The use of flexible feeding strategies should be mediated by prey availability in conjunction with the morphological and behavioral traits of consumers. In our study, prey availability did not appear to be any more limiting in the co-occurring sample than in the segregated samples. Moreover, both fishes in the co-occurring sample consumed some zooplankton. Despite the broad fundamental feeding niches shown by both of these tetradont fishes, gray triggerfish appeared better adapted for feeding on zooplankton. Indeed, Turner and Rooker (2006) surmised that gray triggerfish often consume pelagic copepods, based on Polyunsaturated fatty acid (PUFA) profiles characteristic of phytoplankton-derived particulate organic matter. Perhaps the fusiform shape of gray triggerfish predisposes this fish to feed on zooplankton, as opposed to the more laterally compressed shape of planehead filefish. A fusiform shape should favor rapid forward movements needed for capturing zooplankton and evading predators when making forays away from refuge; whereas a laterally compressed shape should facilitate the required maneuverability for feeding within habitat structure (Alexander 1974).

Coexisting fishes often avoid competition by partitioning food resources (Ross 1986); however, feeding disparities between co-occurring species alone do not imply competition for food (Connell 1980). Food availability did not appear to be limiting for fishes from the co-occurring sample in our study. Furthermore, co-occurring fishes of both species contained relatively more food than fishes from segregated samples. Instead of implying competition, interspecific dietary differences might simply reflect that gray triggerfish were better adapted for consuming zooplankton when the pelagic feeding strategy was relatively profitable (Gerking 1994). Alternatively, interference by planehead filefish might have discouraged gray triggerfish from accessing *Sargassum*-associated epifauna. As a corollary, competition for space within *Sargassum* habitat could explain feeding differences (Cody 1969, Heggnes et al. 1999). Indeed, Chen et al. (2001) documented territorial behavior in connec-

tion with dietary differences among juveniles of 3 co-existing triggerfishes.

Ontogenetic diet shifts have been documented for many species of marine fishes (Munoz and Ojeda 1998). Body-size related changes in food habits reduce diet overlap among size classes, resulting in a broader collective feeding niche (Labropoulou et al. 1997). In our study, ontogenetic shifts were expressed differently between species and ecological settings. In general, ontogenetic diet transitions appeared at a threshold size of about 30 mm SL, the large size class exhibited a narrower diet than smaller size classes, and diets of large segregated fishes were marked by the inclusion of decapod crustaceans. Although diets were only moderately dissimilar among size classes of segregated planehead filefish; distinct diet differences for small co-occurring planehead filefish suggested a broader feeding niche in this setting. In contrast, the feeding niche of gray triggerfish was much narrower within the co-occurring than in the segregated setting. Accordingly, the diets of all size classes of co-occurring gray triggerfish were very similar, mostly due to their common use of pelagic zooplankton.

The extent to which benthic versus pelagic feeding strategies are employed does not map commensurately to effects on epiphytic or pelagic trophic pathways. Many suspension-feeding epifauna depend on phytoplankton-derived particulate organic matter (POM). Indeed, based on PUFA profiles of selected *Sargassum*-associated invertebrates, Turner and Rooker (2006) proposed that the *Sargassum* food web was mainly supported by phytoplankton derived POM. The epiphytic trophic pathway only includes grazers on epiphytic algae and predators of said grazers. The influence of these key tetradont consumers on the structure of *Sargassum* trophic networks should vary accordingly. In conclusion, our study illustrates how the use of benthic versus pelagic feeding strategies by tetradont consumers within the biodiverse and biologically productive *Sargassum* complex is ecologically context-dependent.

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DETERMINATION OF THE SPAWNING SEASON OF BIGMOUTH SLEEPER IN PUERTO RICO BY EXAMINATION OF GONAD MATURATION AND REPRODUCTIVE HORMONE CYCLES

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ABSTRACT: Bigmouth sleepers, *Gobiomorus dormitor*, are diadromous fish that have potential for hatchery production as both food and sport fish and for conservation purposes. Understanding of bigmouth sleeper maturation and seasonal hormone cycling are necessary in order to realize hatchery production. Therefore, seasonal trends in gonadosomatic index (GSI) and plasma vitellogenin, estradiol, progesterone and total testosterone concentrations were examined in wild and captive populations in Puerto Rico during the presumed spawning season. The spawning season for wild river populations of bigmouth sleepers was protracted over several months, but peaks in male testosterone (6.5 ng/mL) and female vitellogenin (11.3 ng/mL), estradiol (3.3 ng/mL), and GSI (9.5–12.0%) demonstrated that the bigmouth sleeper spawning season occurred primarily in July and August in southwestern Puerto Rico. Captive female broodstock held in shallow hatchery ponds demonstrated accelerated maturation, presumably due to warmer water temperatures in the ponds. Therefore, induced and natural spawning attempts using captive female bigmouth sleeper broodstock should be conducted from June through July. However, advanced gonadal maturation and increased testosterone production in captive males was minimal. Hence, induced spawning for captive rearing purposes should use wild broodstock captured during the peak of the natural spawning season in July and August.

KEY WORDS: *Gobiomorus dormitor*, estradiol, progesterone, reproduction, vitellogenin

INTRODUCTION

The bigmouth sleeper, *Gobiomorus dormitor*, is distributed in coastal areas of the Caribbean, northern parts of South America, and the southernmost subtropical United States (Lindquist 1980, Gilmore 1992). Bigmouth sleepers are believed to be amphidromous (Holmquist et al. 1998), with spawning presumably occurring in freshwater streams, followed by larval migration to marine environments, and return to fresh water as juveniles. Because of this life history strategy, construction of impassable dams on rivers impedes bigmouth sleeper movement between freshwater and marine environments. Thus, their life cycle is effectively interrupted, resulting in the extirpation of the species upstream of these impoundments in many river systems (Holmquist et al. 1998). In response to these events, exotic fish species have been introduced to create sport fishing opportunities in the absence of bigmouth sleeper populations (Erdman 1984).

Bigmouth sleepers can survive and grow well in reservoirs and upstream river reaches where juveniles can colonize. In recent decades, three reservoirs in Puerto Rico have periodically supported limited bigmouth sleeper populations, presumably due to dam passage during high flow events (Churchill et al. 1995, Neal et al. 1999). At least one impoundment, Carite Reservoir, supports an abundant, self-sustaining, landlocked population (Neal et al. 2001, Bachelier et al. 2004a). Self-sustaining, landlocked populations also have been reported in Lago de Yojoa, Honduras (Darnell 1962) and Lago Jilao and Lago Apoyo, Nicaragua (McKaye et al. 1979, Bedarf et al. 2001). Thus, bigmouth sleepers appear

to have some plasticity in their life history strategies, and may not require an uninterrupted passage to and from marine systems under certain environmental conditions.

The spawning season, defined as the period in which the majority of reproduction for a population occurs, can be variable for bigmouth sleepers and depends on the water body (lotic vs. lentic) and latitude of the population in question. Previously, the gonadosomatic index (GSI) has been used as a biological indicator of sexual maturation in bigmouth sleepers (Bedarf et al. 2001, Bachelier et al. 2004a). However, assessing gonadal development using classification criteria such as “ripe”, “mature”, or “developed” gonads is vague and not well defined within the literature for bigmouth sleepers. Therefore, these terms are considered to refer to ovaries with oocytes in advanced developmental stages or testes in which spermiation has occurred and the testes have become hydrated.

Bachelier et al. (2004a) found GSI values for bigmouth sleepers in Carite Reservoir increased in April, peaked in May and June, and then declined to base levels by October, although no samples were taken from July through September. Bedarf et al. (2001) assessed the duration of bigmouth sleeper breeding in two lakes in Nicaragua, Lake Jilao and Lake Apoyo. Using GSI values, they reported that mature gonads were found in bigmouth sleeper year-round to varying degrees, and GSI peaked between March and June. In Tortuguero Lagoon, Costa Rica, Kelso (1965) encountered “gravid” females in May. However, “developed” gonads

were reported from March to December in another Costa Rica study (Winemiller and Ponwith 1998), and from April through November in Tecolutla estuary in Veracruz, Mexico (Hernández-Saavedra et al. 2004). Collectively, these findings suggest near year-round or extended spawning periods in some bigmouth sleeper populations.

In addition to examination of GSI values, plasma or serum sex steroid concentrations also can be effective in assessing reproductive development. Hormones such as 17β -estradiol (estradiol) and testosterone have been used to assess reproductive development in multiple fish species (Zohar and Billard 1984, Foster et al. 1993, Holcombe et al. 2000, Davis et al. 2005, Gross et al. 2006), including members of the family Eleotridae (Wang et al. 2001). Vitellogenin has been effective for determining onset of sexual maturation and its continued development in female teleosts, specifically by using an enzyme-linked immunosorbent assay (ELISA) (Jackson and Sullivan 1995, Heppell et al. 1999, Gross et al. 2006). Progesterone also has been used with some success to indicate reproductive maturation in fish (Kagawa et al. 1981, Nagahama et al. 1991, Foster et al. 1993, Gross et al. 2006).

Evidence of natural reproduction in reservoirs, recent management preferences for native species (Clarkson et al. 2005), and the fact that anglers currently target bigmouth sleepers for sport and food (Bacheler et al. 2004b) suggest high potential for this species to serve both sport and food interests in Puerto Rico and elsewhere. Likewise, declines in bigmouth sleeper abundance within its range (Holmquist et al. 1998, Warren et al. 2000) warrant directed conservation efforts for this species. If appropriate hatchery propagation techniques can be developed, supplemental and restoration stocking could become a viable fisheries management and conservation tool for bigmouth sleepers. However, spawning attempts using captive and wild-caught bigmouth sleepers in Puerto Rico have demonstrated minimal success. At present, the major obstacle preventing the development of appropriate bigmouth sleeper spawning protocols is the apparent lack of seasonal reproductive development in captive specimens of reported breeding size (Harris 2007). Thus, to improve bigmouth sleeper spawning techniques, this study examined reproductive hormone cycling and reproductive development for both wild river populations and captive pond populations in Puerto Rico. This information will be used to ascertain the peak times at which induced spawning should be attempted.

MATERIALS AND METHODS

Study area and fish collections

Three free-flowing rivers in Puerto Rico without significant instream barriers to fish migration were used as sources for wild bigmouth sleeper (Figure 1, Table 1). The Rosario River, northeast of the city of Hormigueros, and the Nueve Pasos River, northwest of the city of San Germán, flow into

the Guanajibo River before draining into the Mona Passage south of the city of Mayagüez. The Cañas River drains into the Caribbean Sea on the south central portion of the island near the city of Ponce. Fish were collected using a backpack electrofishing unit using up to 400 volts DC and a 60-Hz pulse cycle. Due to the close proximity, similar physiochemical and habitat characteristics, and stable tropical water temperatures (e.g., summer temperatures 24.8–25.9°C; Kwak et al. 2007) of these rivers, they were considered as one sample population for this manuscript. The amphidromous life history of bigmouth sleepers (Holmquist et al. 1998), proximity of these river systems, absence of significant instream barriers to fish migration, and similar physical and water quality characteristics of these river systems, suggests that population mixing among these river systems is likely to occur.

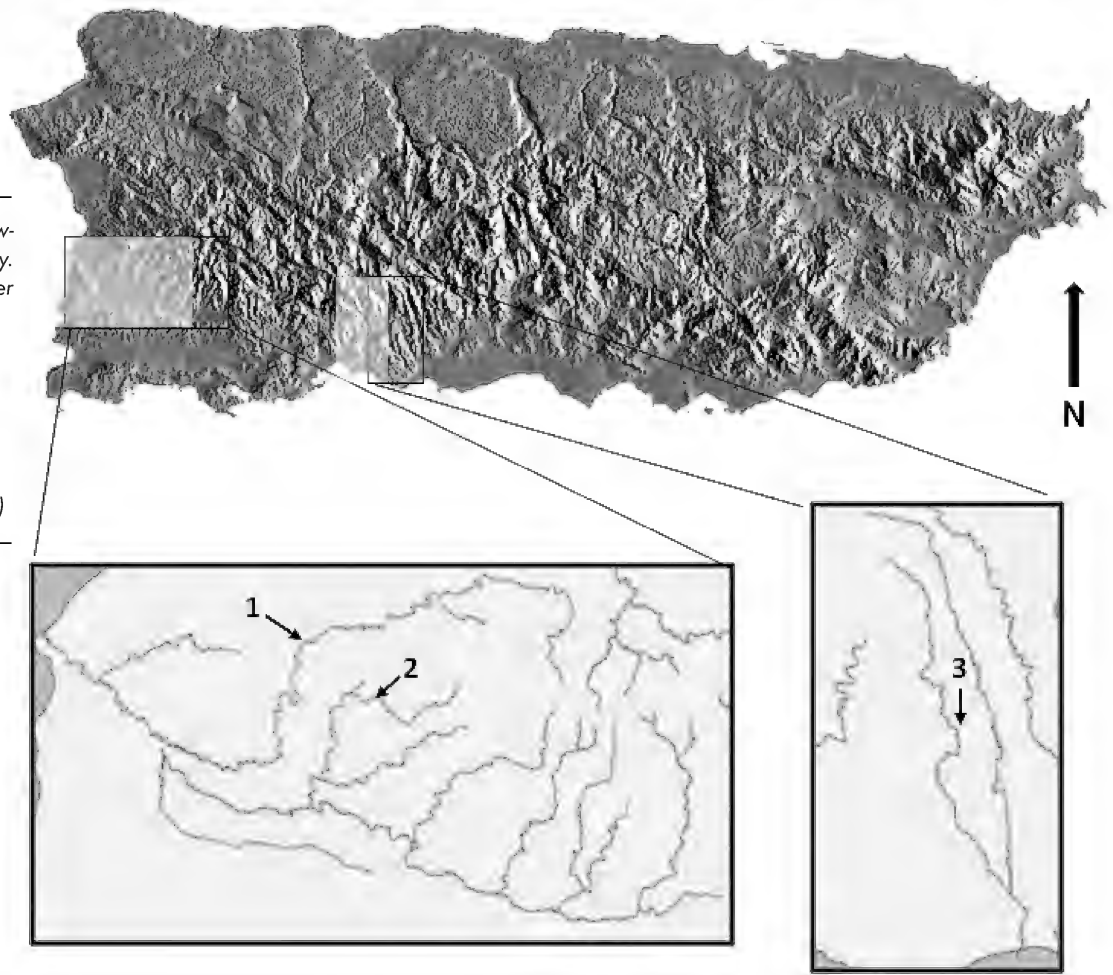
Captive bigmouth sleepers were originally collected at least one year prior to this study from the Cañas, Rosario, and Nueve Pasos Rivers, and from Carite Reservoir. These fish were transported to the Agricultural Research Station of the University of Puerto Rico—Mayagüez located near Lajas, Puerto Rico, and held in four 100 m² ponds with a maximum depth of 1.0 m (summer temperatures 28.1–32.1°C). At least 2 male and 4 female bigmouth sleepers were stocked in each pond. Ponds were stocked with a self-sustaining prey base of mollies *Poecilia* spp., swordtails *Xiphophorus* spp., tilapia *Oreochromis* and *Tilapia* spp., and threadfin shad *Dorosoma petenense*. Sampling was conducted monthly in conjunction with sampling of wild populations using a standard seine. Whereas physiological parameters may change with fish size, bigmouth sleeper total lengths (TL) were compared using general linear models (PROC GLM, SAS Version 9.2) with the class variable month, source (wild or hatchery), and sex.

Gonadosomatic index, plasma vitellogenin, and steroid hormones

Wild bigmouth sleeper specimens collected from the Nueve Pasos, Rosario, and Cañas Rivers between March and October 2007 were used to determine GSI and hormone concentrations before, during, and after the presumed breeding season (May–June; Bacheler et al. 2004a). Each month, 5–7 females and 3–5 males of breeding sizes were collected. All specimens exceeded the reported minimum size at maturity (159 mm and 179 mm TL for male and female bigmouth sleepers, respectively; Bacheler et al. 2004a), and most exceeded 200 mm TL. Fish were measured, weighed (nearest 2.0 g), and euthanized with 150 mg/L of tricaine methanesulfonate (MS-222; Argent Chemical Laboratories, Inc., Redmond, WA) buffered to pH 7 with sodium bicarbonate. Blood (1.0–1.5 mL) was taken by insertion of a sodium heparin coated syringe (21 gauge, 38 mm needle) into the caudal vasculature. In cases where blood collection was insufficient, the tail was severed behind the posterior dorsal fin and blood was collected using 470 μ L heparinized Caraway tubes. Blood samples were immediately placed on ice in 1.5 mL

Figure 1. Map of Puerto Rico showing rivers sampled in this study. The rivers (GPS coordinates of river mouth) were:

- 1) Río Rosario
(18°7'48.76"N, 67°7'59.74"W)
- 2) Río Nueve Pasos
(18°7'1.47"N, 67°4'27.13"W)
- 3) Río Cañas
(17°58'53.34"N, 66°38'16.63"W)



cryotubes coated with ammonium heparin to prevent clotting. Fish specimens were then dissected to remove testis or ovaries, weighed, and GSI calculated according to the equation: $GSI = (\text{gonad weight/body weight}) \times 100$, and is expressed as percent body weight (Murphy and Willis 1996). Due to limitations of the electronic field balance, all gonads weighing less than 2 g resulted in a GSI of less than 0.4, the minimum calculated GSI threshold. Sample collection from captive bigmouth sleepers held in 100 m² ponds at the University of Puerto Rico – Mayagüez's Aquaculture Research Station was repeated as described above for 3–4 male and 3–4 females from March through July. No samples were taken from captive fish after July because no fish were available.

Blood samples were centrifuged at the laboratory to separate the plasma. Plasma was transferred into new cryotubes and frozen at –20°C until transportation on dry ice to the University of Arkansas at Pine Bluff (UAPB) for determination of vitellogenin and hormone concentrations. The samples were immediately frozen at –70°C upon arrival at UAPB. Enzyme-linked immunosorbent assays (ELISA) were partially validated for use in bigmouth sleepers using methods presented in Sink et al. (2008), and then utilized for qualitative determination of plasma 17β-estradiol (Bio-Quant, San Diego, CA), progesterone (Assay Designs, Inc., Ann Arbor, MI), and vitellogenin (Biosense Laboratories,

Bergen, Norway) concentrations. An ELISA kit was also used for the qualitative determination of total testosterone (Assay Designs, Ann Arbor, MI), though no validation procedures were conducted due to monetary constraints. Males were tested for total plasma testosterone concentrations only, while females were tested for plasma estradiol, progesterone, and vitellogenin concentrations.

Vitellogenin and hormone assays

Each assay was conducted as per the instructions provided with the kits except for the vitellogenin assay. The vitellogenin ELISA kit (V01003402) was specific for detection of carp *Cyprinus carpio* vitellogenin, although it has been used for detection of vitellogenin from fathead minnow *Pimephales promelas*, zebrafish *Danio rerio*, goldfish *Carassius auratus*, mullet *Mugil* sp., pinfish *Lagodon rhomboides*, sucker *Catostomidae* sp., and other cyprinids. The monoclonal mouse anti-carp vitellogenin antibody does not react with vitellogenin from striped bass *Morone saxatilis* or brown bullhead *Ameiurus nebulosus* (Biosense kit insert). The monoclonal mouse anti-striped bass vitellogenin antibodies bind vitellogenin from striped bass and rainbow trout *Oncorhynchus mykiss*, and also cross-reacts with vitellogenin from largemouth bass *Micropterus salmoides*, Atlantic cod *Gadus morhua*, Nile tilapia *Oreochromis niloticus*, mummichog *Fundulus heteroclitus*, and sheepshead minnow *Cyprinodon variegatus* (Biosense kit

TABLE 1. Source and sample size of bigmouth sleepers sampled for GSI, plasma vitellogenin and steroid hormone concentrations. No fish remained in the captive population after the July sample.

Month	Number in sample				Source population(s) of wild fish
	Wild		Captive		
	Male	Female	Male	Female	
March	3	7	4	3	Nueve Pasos River and Rosario River
April	3	5	3	3	Cañas River
May	4	7	3	3	Nueve Pasos River
June	3	5	4	4	Rosario River
July	3	5	4	3	Cañas River
August	5	5	—	—	Nueve Pasos River
September	5	6	—	—	Nueve Pasos River
October	5	5	—	—	Nueve Pasos River
Totals	31	45	18	16	

insert). To ensure the greatest probability that vitellogenin from bigmouth sleepers was bound during the assay, monoclonal mouse anti–striped bass vitellogenin antibodies were diluted 1:100 with phosphate buffered saline and 10 μ L of the antibody solution was added to each well of the microplates coated with monoclonal mouse anti–carp vitellogenin antibody. The aqueous solution that contained the antibodies was then evaporated under a gentle stream of nitrogen.

The assay was then run using carp and rainbow trout (V01004301–001) vitellogenin standards and pooled bigmouth sleeper controls. The greatest bigmouth sleeper vitellogenin binding affinity occurred when compared to the carp vitellogenin standard. Since the carp vitellogenin assay is not known to detect rainbow trout vitellogenin, does not bind striped bass vitellogenin, and there is a high probability that a portion of the monoclonal mouse anti–striped bass vitellogenin antibodies were removed during the washing phase, only the unaltered carp vitellogenin ELISA was used for determination of vitellogenin concentrations from bigmouth sleepers during the study.

Because hormone trends were of interest, and not absolute concentrations, only partial validations were conducted for the vitellogenin, estradiol, and progesterone assays to determine the suitability of the kits for detecting hormonal shifts in bigmouth sleepers. The samples were thawed and 150 μ L of plasma from 3 males were pooled and used for the male standard and 5 females were pooled and used for the female standard to validate each kit. All samples were run in duplicate for the validation procedures and sample hormone determination. Validation tests followed the Validation of Analytical Procedures: Methodology (FDA CVM 1999) and were similar to validation tests used in Barry et al. (1993) for a cortisol ELISA. Accuracy was tested by calculation of recoveries from samples spiked with known amounts of hormones (3 increments of the hormone standards provided with the kits). Precision was tested by repeated assays of samples (8 times in duplicate) on the same plate and by calculation of

coefficient of variation (% CV). Mean sample recovery percentage limits of within 90–110% were defined as meeting validation criteria. A percent coefficient of variation of ≤ 20.0 was set as the acceptable limit for the intra–assay % CV.

Statistical analyses

Plasma vitellogenin, steroid hormone concentrations, and GSI values were plotted over time to illustrate monthly trends in reproductive development, and to examine relationships

between gonad maturation and hormone levels. To determine significant monthly trends, one–way analysis of variance (ANOVA) was used unless data failed normality, in which case Kruskal–Wallis non–parametric test of ranks was employed. In either test, month served as the main effect. The Kolmogorov–Smirnov test (with Lilliefors' correction) was used to test data for normality. Pair–wise multiple comparisons were used to separate months. Differences in GSI, hormone and vitellogenin concentrations of wild and captive populations were analyzed using a Student's *t*–test conducted by month. In cases where normality tests failed, analyses were conducted using a Mann–Whitney Rank Sum Test. These tests were chosen over paired data tests because periodicity of peaks was of interest, and may not have been discerned by a paired–*t* test or ANOVA on repeated measures. A Pearson product–moment correlation coefficient was used to analyze correlation of hormones and GSI for individual fish. Data for GSI were transformed by taking ArcSine of the square root as per Osborne (2002). Statistical significance for all tests was set at an alpha level of 0.05 (Zar 1999).

RESULTS

Fish characteristics

A total of 57 wild female bigmouth sleepers and 31 wild male bigmouth sleepers were collected for this study. Mean \pm se size of wild–caught females was 226 ± 3 mm TL and 100 ± 4 g; wild–caught males averaged 271 ± 10 mm TL and 185 ± 23 g in size. Sixteen captive females and 18 captive males were sacrificed for this research. Captive females averaged 253 ± 11 mm TL and 134 ± 16 g, and captive males averaged 270 ± 13 mm TL and 156 ± 22 g. The general linear model indicated that differences in fish TL occurred (Overall model: $F_{12,51} = 5.71$, $p < 0.0001$, $r^2 = 0.57$), with month ($F_3 = 6.02$, $p = 0.0014$, $r^2 = 0.10$) and sex ($F_1 = 20.84$, $p < 0.0001$, $r^2 = 0.34$) contributing to the observed variability. Total length

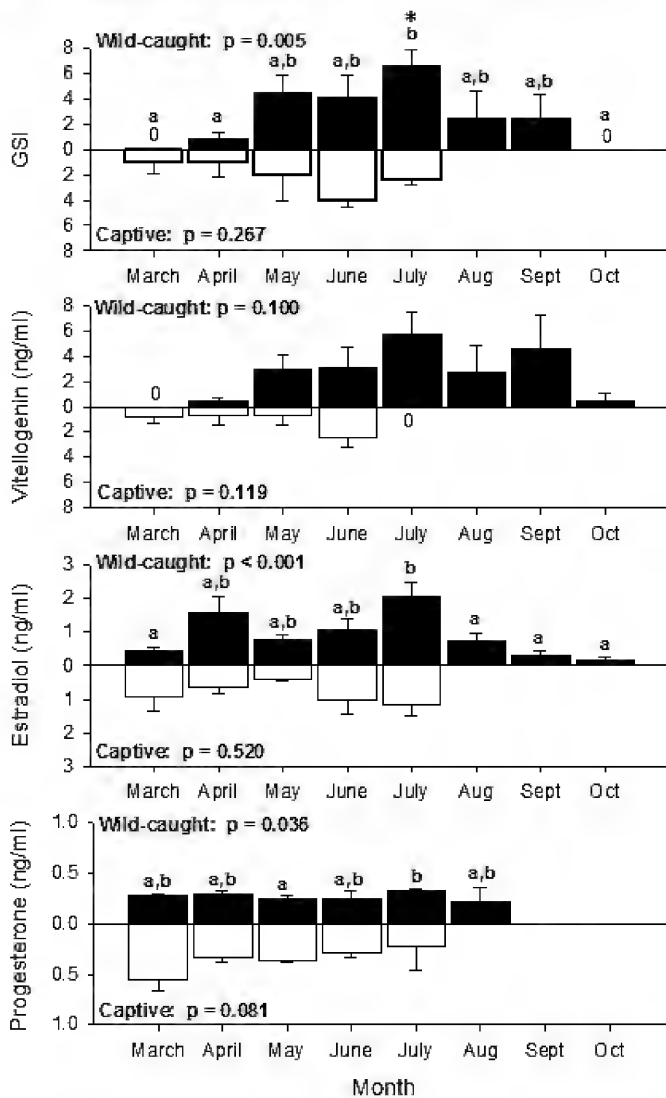


Figure 2. Comparison of gonadosomatic index (GSI), plasma vitellogenin and steroid hormone concentrations in female bigmouth sleepers from wild-caught (solid bars) and captive (open bars) populations. GSI (gonad weight/body weight $\times 100$), vitellogenin (ng/mL), estradiol (ng/mL), and progesterone (ng/mL) are presented. Progesterone was not measured in wild-caught fish in September and October. No captive fish remained after July samples. Error bars represent standard errors (se). The p -values reflect analysis of variance among months for each population, with pair-wise comparisons indicated with lowercase letters. Individual months that differed between wild-caught and captive fish are indicated with an asterisk (*).

did not differ significantly between wild versus hatchery fish ($F_1 = 3.03$, $p = 0.0880$, $r^2 = 0.04$).

GSI

Wild-caught females showed clear temporal trends in GSI during spring and summer ($F_{7,37} = 6.36$, $p < 0.001$). Values for GSI were below the minimum calculated GSI threshold of 0.4 in March samples, but increased from April through June, and peaked in July before declining in August and September to baseline levels in October (Figure 2). Minimum individual values for each month were below the minimum calculated GSI threshold of 0.4, and maximum

individual values reached peaks in May through September of 9.5–12.0. Conversely, captive females had greater GSI values in March than wild females, which moderately increased in April and May before peaking in June, then dropped to nearly half the peak value in the final samples of captive fish in July (Figure 2). However, this trend was not statistically significant ($F_{4,11} = 1.837$, $p = 0.192$). Minimum individual values of captive fish in every month were below the minimum calculated GSI threshold of 0.4, and maximum individual values peaked at nearly 6.0 for May and June. Monthly comparisons of wild-caught versus captive females found only one significant difference in GSI that occurred during July ($t_6 = 2.58$, $p = 0.042$; Table 2).

Wild-caught males had baseline GSI values below the minimum calculated GSI threshold of 0.4 for both March and April samples, followed by slight increases from May through June, peaking in July before decreasing to baseline values again in August ($F_{7,23} = 16.94$, $p < 0.001$; Figure 3). A slight increase of GSI values was observed in September with a final decrease in gonadal development in October. Minimum individual values were below the minimum calculated GSI threshold of 0.4 for every month. Peak measurements for individuals were observed in June and July at 2.0 and 2.7, respectively. Captive males showed no discernable gonad development throughout the study, and no significant difference between wild and captive male GSI was found in any month, although differences approached significant levels in March, June, and July (Table 2).

Vitellogenin

The ability of the carp vitellogenin kit to accurately detect bigmouth sleeper vitellogenin was low in the range of samples tested (mean recovery of samples spiked with 5, 10, or 15 ng/mL = 84.4%). The precision of sample detection and ability to reproduce results from the same sample were within the established limits (%CV < 20%) for the validation (mean inter-assay %CV = 18.9%; mean intra-assay %CV = 11.3%; range 2.3–25.8%).

Plasma samples from wild-caught female bigmouth sleeper contained no detectable vitellogenin concentrations in March, followed by a steady increase in mean vitellogenin from April through June before peaking in July (Figure 2). Vitellogenin concentrations decreased from August to near initial concentrations by October. Minimum individual female vitellogenin concentrations were 0.0 for every month, and maximum concentrations for individual females reached 10.4, 11.3, and 17.0 ng/mL for July, August and September, respectively. There was no apparent relationship between fish size and maximum vitellogenin measurements. Statistical analysis did not indicate differences between months for vitellogenin ($F_{5,26} = 2.05$, $p = 0.100$) despite an obvious trend graphically. This anomaly was likely the result of the low sample sizes in conjunction with the high variability in the data.

Plasma samples from captive females contained greater

concentrations of vitellogenin in March compared to wild fish, maintaining averages just below 1.0 ng/mL every month until June, when it peaked before dropping to 0.0 in July (Figure 2). Minimum individual female vitellogenin concentrations were 0.0 for every month except June, which had a minimum sample concentration of 1.4 ng/mL. Maximum concentrations for individual females ranged from 1.7 to 3.7 ng/mL from March through June. Monthly comparisons suggested no significant differences in vitellogenin concentrations between wild and captive populations (Table 2). However, wild-caught bigmouth sleeper in July had much greater concentrations than captive fish, and approached statistical significance ($t_6 = -2.35$, $p = 0.057$).

Estradiol

The ability of the estradiol kit to accurately detect bigmouth sleeper estradiol was acceptable in the range of samples tested (mean recovery of samples spiked with 1, 3, or 10 ng/mL = 90.0%). However, the precision and ability to reproduce results from the same sample did not fall within the established limits (%CV < 20%) for the validation (mean inter-assay %CV = 21.7%; mean intra-assay %CV = 16.8%, range 6.4–22.8%).

Plasma samples from wild-caught females contained low concentrations of estradiol in March and exhibited a slight increase in April (Figure 2). This trend was followed by a decline in plasma estradiol concentrations in May before concentrations peaked in July (Figure 2). Another decline in estradiol concentrations began in August, which led to low concentrations in September and October. Minimum individual estradiol concentrations never dropped below 0.05 ng/mL, which was found in October. Maximum readings for individual fish were 3.5 and 3.3 ng/mL, respectively; minimum and maximum values were recorded in April and July, respectively.

Captive female bigmouth sleeper contained greater plasma estradiol concentrations in March than wild fish, and exhibited a decline in concentrations through April and May before increasing in June and peaking in July (Figure 2). The minimum individual plasma estradiol concentration was 0.3 ng/mL from a female sampled in May. Maximum plasma estradiol concentrations for individual fish were 1.8 and 1.9 ng/mL for March and June, respectively. Monthly

TABLE 2. Statistical results for comparisons of reproductive development indicators between wild and captive bigmouth sleeper populations. Test statistic (T) represents a Mann–Whitney Rank Sum Test used when normality or equal variance tests failed. A Student's t -test statistic (t) was used when normality and equal variance tests passed. **Bold type** indicates statistical significance at alpha level of 0.05. There were no captive fish remaining after July, so further comparisons were not possible.

Month	Female	Male	Vitellogenin	Estradiol	Progesterone	Testosterone
	GSI	GSI				
March	$T = 20.000$ $p = 0.517$	$T = 18.000$ $p = 0.057$	$T = 18.500$ $p = 0.143$	$t = 1.500$ $p = 0.133$	$T = 11.000$ $p = 0.133$	$t = 3.742$ $p = 0.013$
April	$T = 14.000$ $p = 1.000$	$T = 6.000$ $p = 0.100$	$T = 14.000$ $p = 1.000$	$t = 1.309$ $p = 0.238$	$t = 0.953$ $p = 0.384$	$t = 0.267$ $p = 0.802$
May	$t = 1.267$ $p = 0.241$	$T = 7.500$ $p = 0.114$	$t = 1.166$ $p = 0.277$	$t = 1.511$ $p = 0.169$	$T = 24.000$ $p = 0.117$	$t = 0.260$ $p = 0.808$
June	$t = 0.582$ $p = 0.579$	$T = 18.000$ $p = 0.057$	$t = 0.309$ $p = 0.768$	$t = 0.106$ $p = 0.919$	$t = 0.550$ $p = 0.611$	$t = 1.025$ $p = 0.363$
July	$t = 2.584$ $p = 0.042$	$T = 18.000$ $p = 0.057$	$t = 2.351$ $p = 0.204$	$t = 1.425$ $p = 0.204$	—	$t = 4.033$ $p = 0.010$

comparisons between wild and captive populations found no significant differences in estradiol concentrations ($p > 0.05$) (Table 2).

Progesterone

The ability of the progesterone kit to accurately detect bigmouth sleeper progesterone was acceptable (mean recovery of samples spiked with 1, 5, or 10 ng/mL = 94.4%). The precision and ability to reproduce results from the same sample was within the established limits for the validation (mean inter-assay %CV = 12.9%; mean intra-assay %CV = 9.8%, range 1.2–13.7%).

Wild-caught female bigmouth sleeper showed no discernible trends in plasma progesterone concentrations, averaging between 0.2 and 0.3 ng/mL throughout the study (Figure 2). The minimum and maximum progesterone concentrations for individual bigmouth sleeper were 0.1 and 0.5 ng/mL, respectively. Both minimum and maximum values were recorded in August. Captive female bigmouth sleeper showed slightly more variation in progesterone concentrations, ranging from 0.3 to 0.6 ng/mL, with a steady decline from March to July, though the trend was not statistically significant ($H_4 = 8.31$, $p = 0.081$) (Figure 2). The minimum and maximum plasma progesterone concentrations for individual captive fish were 0.2 and 0.7 ng/mL, respectively; minimum and maximum values were recorded in June and March, respectively. Monthly comparisons of wild and captive populations found no significant differences in progesterone concentrations (Table 2). Due to no discernable trends in progesterone data, no testing was conducted for progesterone in September and October.

Testosterone

Plasma testosterone concentrations (mean intra-assay %CV = 8.4%, range 0.6–14.2%) in wild-caught male big-

mouth sleeper steadily increased from March to June before increasing rapidly in July (Figure 3). Mean testosterone concentrations peaked in August and September before declining in October. Minimum and maximum testosterone concentrations for individual fish were 0.3 and 6.5 ng/mL, respectively; minimum and maximum values were recorded in March and August, respectively.

Captive male bigmouth sleeper showed little variation in plasma testosterone concentrations for the duration of the study, with monthly averages ranging from 0.6 to 0.8 ng/mL. Minimum and maximum values for individual fish were 0.3 and 0.9 ng/mL, respectively; minimum and maximum values were recorded in April and March, respectively. Comparisons of testosterone concentrations in wild-caught versus captive bigmouth sleeper indicated significant differences in both March and July (Table 2). In March, the average testosterone concentration for captive fish was twice that of wild fish ($t_5 = 3.74$, $p = 0.013$). In July, testosterone concentrations in wild fish peaked and averaged more than four times that of captive male testosterone concentrations ($t_5 = -4.03$, $p = 0.010$).

Pearson product-moment correlation coefficient

For wild-caught bigmouth sleeper, significant positive correlations over time were detected between female GSI and vitellogenin ($r = 0.90$, $p < 0.001$) and estradiol ($r = 0.47$, $p < 0.001$), but not for progesterone ($r = -0.24$, $p = 0.151$). Vitellogenin production was positively correlated with estradiol concentration ($r = 0.28$, $p = 0.033$), but not progesterone concentration ($r = -0.25$, $p = 0.123$). Estradiol concentration was not correlated with progesterone concentration ($r = -0.13$, $p = 0.445$).

DISCUSSION

Seasonal trends in GSI and plasma vitellogenin, estradiol, and total testosterone concentrations indicated that the spawning season of bigmouth sleepers is protracted over several months, but occurs primarily in July and August in wild river populations of southwestern Puerto Rico. For female bigmouth sleepers, vitellogenin concentrations and GSI values peaked in July, while estradiol concentrations showed a bimodal distribution. Estradiol peaked in April and again in July coincident with the peak of GSI values. The bimodal pattern of estradiol secretion found in this study corresponded to an initial increase prior to vitellogenesis and gonadal development (as indicated by GSI) and a second increase prior to presumed spawning. This bimodal pattern of estradiol secretion has been documented in other fish species (Jackson and Sullivan 1995). The correlation between estradiol, vitellogenin, and GSI were anticipated with ovarian development preceding spawning, and is attributed to vitellogenesis induced by secretion of estrogen. The secretion of estradiol during ovarian development stimulates vitellogenin synthesis in the liver. Vitellogenins are integrated into developing

eggs as phosvitin and lipovitellin, resulting in increased ovarian size and GSI (Davis et al. 2005). Data from this study similarly indicate the same progression with an increase in estradiol secretion followed by simultaneous increases in vitellogenin production and GSI.

The lack of any noticeable increase in production of total progesterone during this study was enigmatic, as Zohar and Billard (1984) reported several periods of increased progesterone-derived 17α -hydroxy- 20β -dihydroprogesterone during the maturation cycles of fish. While the assay kit used to detect progesterone was only 3.46% cross-reactive with 17α -hydroxy- 20β -dihydroprogesterone, increased progesterone secretion would be likely in response to elevated 17α -hydroxy- 20β -dihydroprogesterone, as it is the primary precursor to this hormone. However, no such increases in progesterone production were noted in this study. Perhaps although concentrations of 17α -hydroxy- 20β -dihydroprogesterone undergo several changes during fish gonad maturation

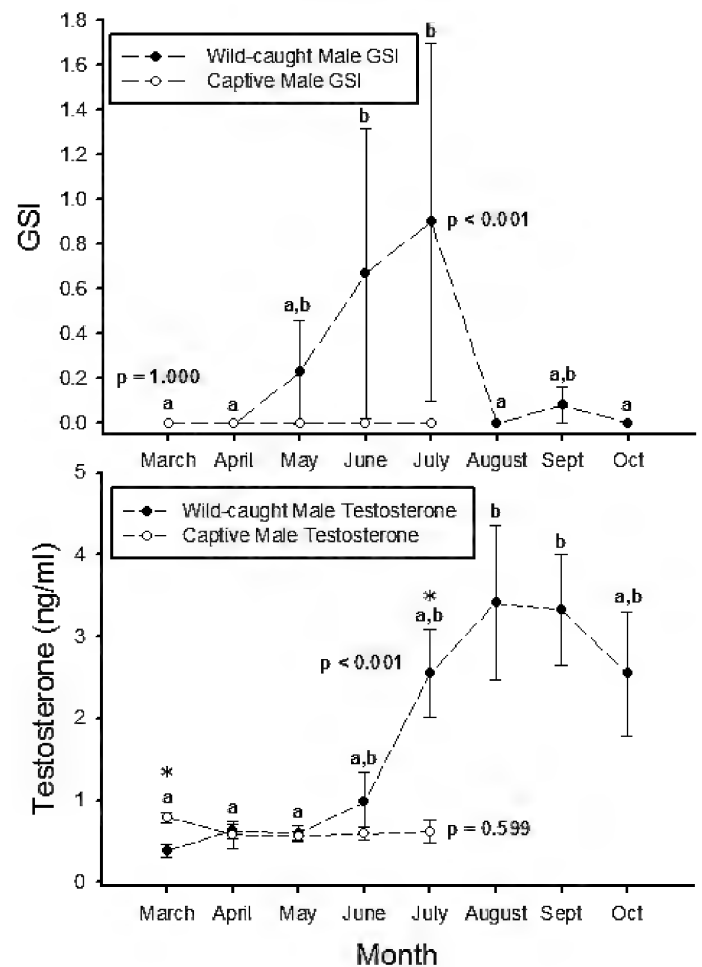


Figure 3. Comparison of gonadosomatic index (Top; GSI = gonad weight/body weight $\times 100$) and plasma testosterone concentrations (Bottom) in wild-caught and captive male bigmouth sleepers. Error bars represent standard errors (se). The p -values reflect analysis of variance among months for each population, with pair-wise comparisons indicated with lowercase letters. Individual months that differed between wild-caught and captive fish are indicated with an asterisk (*).

tion, concentrations of its precursor progesterone remain relatively unchanged in bigmouth sleepers. Significant increases in progesterone concentrations just prior to final maturation may have been missed, as we were unable to collect any females that were in the final stages of maturation or about to undergo ovulation. 17 α -hydroxy-20 β -dihydroprogesterone is often only apparent for short durations during maturation and easily could have been missed. Very little is known about maturation or hormone cycling in bigmouth sleepers, so it may be possible that progesterone is not a maturation hormone in this species.

Wild male bigmouth sleeper GSI peaked in July and dropped to below the minimum calculated GSI threshold of 0.4 in August, but testosterone concentrations continued to increase in August before gradually decreasing through September and October. One explanation for this was that total testosterone production was actually measured, not specifically 11-ketotestosterone. 11-ketotestosterone is the primary sexual steroid responsible for gonadal maturation in male teleost fish and the greatest concentrations of 11-ketotestosterone have been recorded just prior to the start of spermiation (Zohar and Billard 1984). Production of 11-ketotestosterone may have declined following the GSI peak in July, though total testosterone continued to increase. Male bigmouth sleepers are nest guards (McKaye et al. 1979) and the increased production of total testosterone may be a physiological response to territorial defense and nest guarding activities.

The primary environmental stimulus for reproductive development in females appeared to be water temperature. Captive fish held in warm ponds (March temperature = 27.8°C) demonstrated earlier development than wild fish in cooler rivers (March temperature = 23°C). In Carite Reservoir, peak reproductive development was intermediate to ponds and rivers, which would be expected based on the surface temperature of 26°C recorded by Bachelier (2002) on 6 April 2001, about two weeks later in the year than the March data from this study. Bachelier et al. (2004a) also reported peak GSI values in May and June, indicating that spawning occurred during these months.

Lack of male development in ponds, relative to wild fish, as indicated by lower GSI and testosterone concentrations

suggests that males may require another stimulus for reproductive development not present in ponds, such as increased water discharge. The importance of elevated discharge to spawning behavior has been documented for Hawaiian gobies and eleotrids (Fitzsimons et al. 2002). This hypothesis is further supported by data showing greater numbers of bigmouth sleeper larvae were collected in the wet season than in the dry season during sampling in the Tecolutla River in Veracruz, Mexico (Hernández-Saavedra et al. 2004). It may be possible to artificially provide this stimulus in a hatchery situation, and further research on this concept is warranted.

The sample sizes used during this study were relatively small due to the remote location, decline in native populations, and difficulty in collection of mature specimens. Similarly, captive fish sample sizes were limited because of low fish availability, as all captive broodstock at the Aquaculture Research Station were sacrificed for this research. Despite low sample sizes, the statistical design maintained enough power (> 0.8) to determine statistically significant differences in hormone concentrations at monthly sampling intervals. While more samples may be needed to truly characterize hormonal changes during the bigmouth sleeper spawning season, the data gathered nonetheless allow for determination of when spawning cycles were initiated and when peak spawning periods for bigmouth sleepers occurred on the island of Puerto Rico.

The spawning season for wild river populations of bigmouth sleepers is protracted over several months, but appears to peak in July and August in southwestern Puerto Rico. Captive female bigmouth sleeper broodstock held in shallow hatchery ponds matured earlier in the season likely because of accelerated environmental stimuli, increased water temperatures in particular. Therefore, induced and natural spawning attempts for captive bigmouth sleeper broodstock should be conducted in June through July, while wild broodstock should be collected and spawned in July and August. However, as gonad development of captive male bigmouth sleeper requires an additional stimulus that is presently unknown, collection and spawning of wild broodstock is currently the only viable option for bigmouth sleeper propagation.

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An Evaluation of Mississippi Barrier Islands as a Spawning and Nesting Habitat for the American Horseshoe Crab, *Limulus polyphemus*, with Implications for Island Restoration

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AN EVALUATION OF MISSISSIPPI BARRIER ISLANDS AS SPAWNING AND NESTING HABITAT FOR THE AMERICAN HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, WITH IMPLICATIONS FOR ISLAND RESTORATION

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ABSTRACT: The American horseshoe crab (HSC), *Limulus polyphemus*, is an economically and ecologically important species in the coastal ecosystem. Horseshoe crabs inhabit the continental shelf and estuaries from Maine to the central Gulf Coast and the Yucatán Peninsula. Although the presence of horseshoe crabs in southern Mississippi is known locally, there are limited data specific to the area and population, particularly regarding spawning and nesting habitat. Surveys of HSC presence, habitat use, and behavior on Mississippi barrier islands were conducted between March and November 2007 to 2009. These data, combined with habitat surveys of the barrier islands, were used to characterize HSC use of these islands. Horseshoe crabs were present on barrier island beaches from March to November, but active spawning and nesting occurred primarily in April and May. Peak abundance varied by year but not between islands surveyed. Nesting activity was only observed on the north side of both islands and was generally clustered in areas with a mild elevation profile. In comparison to other studied populations both in the Gulf of Mexico (GOM) and along the U.S. Atlantic coast, HSC nesting on Mississippi barrier islands followed generally similar patterns, but did display some important differences. Nesting was highest in low energy, well oxygenated habitat, which included the sub-tidal sand flats that are common along these islands. In addition, HSC are smaller than the range-wide mean reported in the literature, but that may be related to these islands being close to the edge of the reported HSC range in the GOM. The continued existence of HSC in Mississippi appears tied to their preference for barrier island beaches as spawning and nursery habitat. More research is needed, but this study documents that the distribution of HSC nesting habitat includes Mississippi beaches and this should be considered as a part of restoration plans being evaluated for these barrier islands.

KEY WORDS: *Limulus*, habitat, nesting, restoration

INTRODUCTION

The American horseshoe crab, *Limulus polyphemus*, is an economically and ecologically important invertebrate in United States coastal waters. American horseshoe crabs (HSC) are harvested for bait in the eel and conch fisheries (Shuster et al. 2003), extraction of *Limulus* amoebocyte lysate (LAL) to screen for endotoxins is a multi-million dollar biomedical industry (Berkson and Shuster 1999), and research focusing on the crab's compound eyes has resulted in many medical advances in the structure and physiology of vision (Battelle 2006). Horseshoe crab eggs are also managed as a valuable nutrient-rich food source for a variety of migrating sea birds (Castro and Meyers 1993, Shuster et al. 2003) and the threatened loggerhead turtle, *Caretta caretta* (Keinath et al. 1987).

American horseshoe crabs are distributed along the U.S. Atlantic coast and in the Gulf of Mexico (GOM) (Shuster 1982, Anderson and Shuster 2003). In the Gulf, they have been documented from the Florida Keys north to Mobile Bay, AL and on the coast of the Yucatan Peninsula (Sekiguchi and Shuster 2009). American horseshoe crab populations and their impacts on the Atlantic ecosystem have been extensively researched; however, populations in the northern GOM have not. In particular, although the presence of HSC has been acknowledged in Mississippi (Richmond 1962,

Shuster and Sekiguchi 2009), this is not a formally recognized portion of the species' range, and there is a deficit of information specific to this region.

A key component of population distribution for HSC is the availability of beach nesting habitat (Brockmann 2003, Shuster and Sekiguchi 2009). In the spring, mature HSC begin moving from deeper water toward sandy beaches where spawning occurs and females deposit their eggs to be fertilized and develop buried in the sand (Brockmann 2003). The larvae and juveniles then recruit to nearshore benthic habitat (e.g., sand flats, seagrass beds) for much of their first year of life (Gilbert and Clark 1981, Carmichael et al. 2004). Adult HSC habitat is in deeper water, so the existence of quality spawning and nursery habitat has been suggested as a key limiting factor for their distributional range in coastal ecosystems (Sekiguchi and Shuster 2009).

In areas of the northern GOM west of Mobile Bay, particularly Mississippi Sound (Sound), intertidal sandy beach habitat is highly limited in spatial extent. Excepting artificially maintained beach, intertidal sandy beach habitat is almost exclusively found on the four barrier islands forming the southern boundary of the Sound. Artificially maintained beach has been used as nesting habitat by HSC in other regions (Jackson et al. 2005), however artificial beach in our

study area is closer to shore and subject to much lower salinities and much higher human traffic than the barrier islands. The barrier islands may therefore be critical habitat for HSC at the previously undocumented western boundary of their range in the northern GOM. Mississippi barrier islands are composed of four outer islands, 15–20 km offshore, and two inner islands about 10 km off the coast. In particular, West Ship Island and Horn Island form most of the southern boundary of the Sound and are of interest with regards to HSC habitat, as these islands are a part of the Gulf Islands National Seashore and therefore protected from major human-induced changes. If these islands contain critical HSC spawning habitat then this would be one of the ecosystem services of these federally protected islands and would have to be considered as a part of any alteration plans for these islands.

Horseshoe crabs show a significant level of plasticity in spawning/nesting habitat choice. The seasonal patterns of activity differ between geographically separate populations of HSC, and physical and behavioral characteristics of multiple populations are not identical (Shuster 1982, Brockmann 2003, Mattei et al. 2010). Spawning/nesting behavior is best documented along the U.S. Atlantic coast and the coast of Florida in areas with semi-diurnal tides (Rudloe 1985, Shuster and Botton 1985, Penn and Brockmann 1994). Nesting by HSC has been documented in microtidal systems (Ehlinger et al. 2003), but both Brockmann (2003) and Sekiguchi and Shuster (2009) suggest that tidal amplitude and period is a primary determinant of HSC distributional range through its effects on nesting behavior. Yet, if HSC use the Mississippi barrier islands as nesting habitat, then the reduced tidal range, high wind influence of tides, and the general lack of sandy shoreline along the Mississippi coast may result in key regional differences in spawning and nesting behavior for HSC that need to be accounted for in protecting habitat.

The purpose of this study was to: 1) document HSC spawning and nesting activity on Mississippi coastal islands; 2) Investigate seasonal changes in relative population abundance of adult spawning using catch per unit effort (CPUE) analysis; and 3) identify preferred habitat characteristics of spawning adult horseshoe crabs along the Mississippi coast and compare these results to reports on HSC nesting habitat from other regions. To facilitate objective three, habitat data were collected using commonly cited habitat characteristics from other areas including environmental conditions, sediment characteristics, and beach topography. These outcomes will allow for a better understanding of local habitat dependencies of this species.

MATERIALS AND METHODS

Sampling Location and Period

All sampling occurred on Horn (lat 30°13'57.0"N, long 88°40'21.7"W) and West Ship (lat 30°12'29.1"N, long 88°57'45.6"W) Islands, which together form most of the

principal southern boundary of the Sound (Figure 1a). Sampling was conducted between March and November in 2007–2010, and occurred bi-monthly within 48 hours of the new and full moon at or near high tide. The islands were divided into north and south sites (Figure 1). Samples collected on Horn Island were limited to the western half of the island due to limited accessibility. All sampled sandy beach areas met generally-cited requirements for suitable HSC spawning habitat, (e.g., sandy sloping shoreline; Shuster and Sekiguchi 2009).

Biological Data Collection

Data on spawning activity was gathered by counting HSC on both islands along a randomly selected 1 km transect of shoreline on each date. All HSC encountered between the Mean High Water Line (MHWL) and a water depth of 100 cm were counted and measured. Parameters collected for each animal included sex, prosomal width (mm), state (paired, unpaired, dead, or exuviae), water depth (cm), and distance from shore (m). Sex was determined by presence or absence of modified pedipalps. Sex ratio was estimated for each survey based on all crabs examined and was summarized based on the mean by island and year. Catch per unit effort (CPUE/km) was used as an index of HSC abundance for comparisons between and within islands.

Beach Sediment Composition

Sediment composition analysis was based on sediment cores taken with a 5 cm diameter PVC pipe to a 30 cm depth. Cores were taken every 2 km on the north side of West Ship Island (~10 km, $n=5$) and at 3 randomly located sites on the south side of West Ship Island (Figure 1b). Horn Island has an approximate perimeter length of 40 km; therefore, sites at Horn Island were selected on both the northern and southern shores, but they were concentrated along the western end of the island (Figure 1c). Core sites were characterized based on the HSC abundance data collected in 2007–2009 as sites of high ($> 50/\text{km}$), low ($1\text{--}49/\text{km}$), and no presence of HSC. At each site, 4 cores were taken in each of 2 strata; just below the high tide line on the beach, and 10 m seaward of the tide line. The 4 cores from each site were thoroughly mixed by sifting them together.

Particle size was determined from a 60 g (dry weight) subsample taken from the composite cores and disaggregated using a mortar and pestle. Particle size distribution was estimated by mechanically sifting the samples for 15 min through a series of graduated sieves ranging from 63 μm (4 ϕ , #230) to 1600 μm (–1 ϕ , #5) at 1.0 ϕ intervals (Boggs 1987). Particle sizes are defined according to Boggs (1987) as 1 ϕ = $-\log_2(S)$ where S is the particle size (mm). The particles that were retained on the sieve screens were weighed (g) and converted to a percentage in each size class for each composite sample.

Non-sand composition of sediment samples was estimated in 2 categories representing calcium-based material such

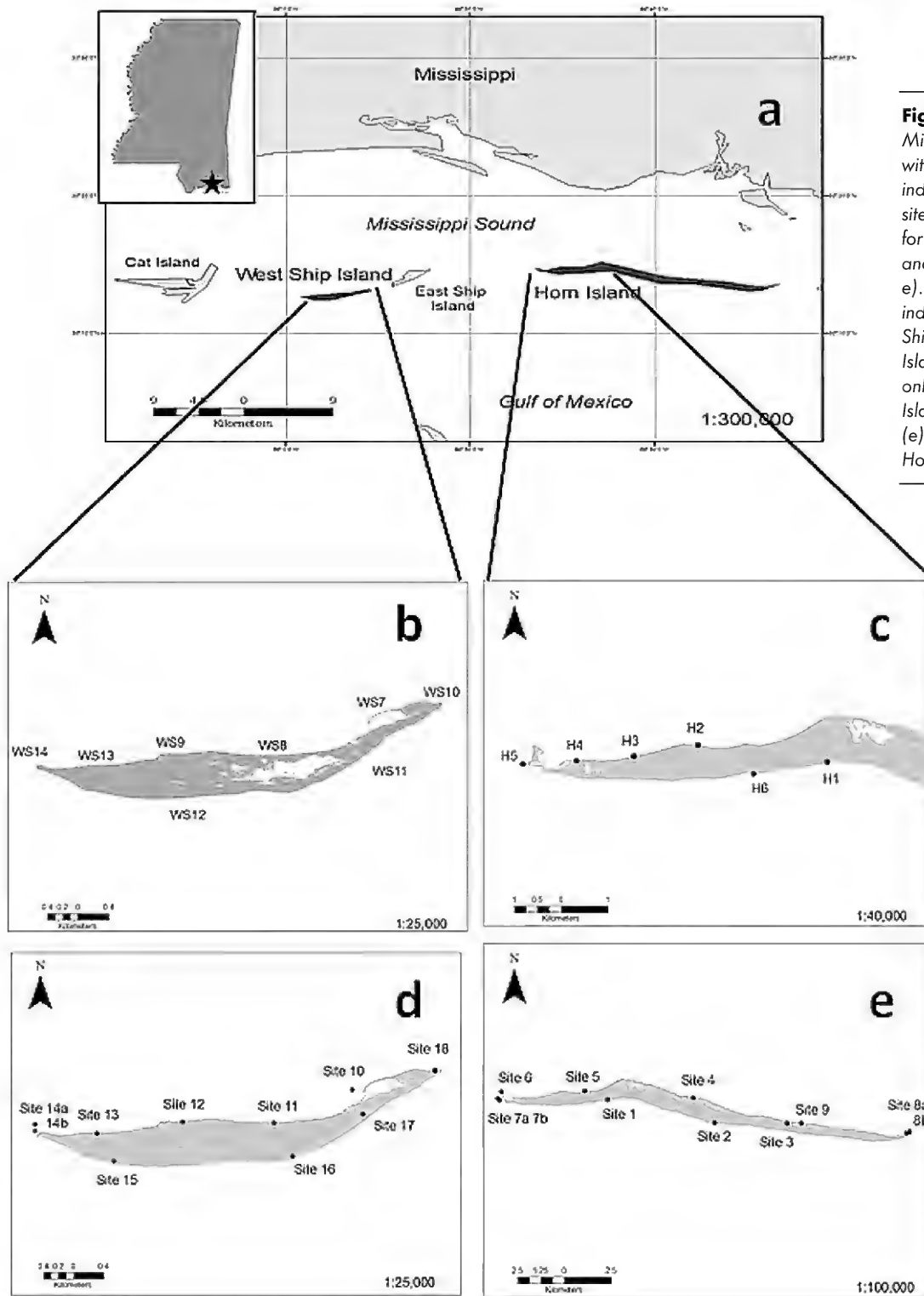


Figure 1. Map of coastal Mississippi study area (a) with islands used for this study indicated in black. Collection sites on each island are given for habitat sampling (b & c) and beach topography (d & e). Sample collection sites are indicated separately for West Ship Island (b & d) and Horn Island (c & e). Panel (c) shows only the western end of Horn Island for clarity while panel (e) shows the entire length of Horn Island.

as shell or gravel (shell hash) and organic content. Percentage composition of shell hash was determined by the addition of 10% HCl to a second 60 g (dry weight) disaggregated sample until the reaction (off-gassing) ended. The reacted samples were then rinsed with tap water and dried at 95°C to a constant weight (0.01 g). The difference between initial dry weight and acid-washed dry weight was classified as shell hash weight. Percentage organic composition (e.g., detritus,

living organisms) of the sediment was determined from a separate 3 g (dry weight) sub-sample taken from each stratum composite core. The sub-sample was dried at 95°C and weighed to the nearest 0.01g. The samples were then placed in a muffle furnace at 550°C for two hours and cooled in a desiccator. The cooled samples were weighed (g), and the percent difference between sample dry weight (g) and post-muffle weight (g) was recorded as the organic content (%).

Beach Topography

Depth to Reducing Layer (DRE) measures the vertical height of the oxygenated sediment suitable for nesting (Thompson 1999). The transition from normoxic to anoxic sediment is clearly visible as a change from light to dark coloration. This can be compared to direct estimates of sediment oxygen levels re-parameterized to a normoxic/anoxic delineation, and was chosen as it is simpler and does not require an oxygen meter. Beach DRE samples were collected in May 2010 by taking core samples along multiple 100 m transects running seaward perpendicular to the high tide line. The sites selected on Horn and West Ship Island corresponded with the sites sampled for sediment analysis (Figure 1b, c). A single core was taken every 10 m along the 100 m transect using a clear acrylic tube. The depth from the core surface to the beginning of the visible reducing zone, indicated by a transition to dark grey sediment, was measured (cm). A profile was composed showing the location of the reducing zones.

Beach slope was measured perpendicular to the Extreme High Tide Line (EHTL) every 2 km on West Ship Island (Figure 1d) and every 10 km on Horn Island (Figure 1e) out to 100 m or until water depth interfered with measurement. Two poles (1.5 m height) marked in 1 cm increments were placed perpendicular to the beach 1.5 m apart. The landward observer's eye was aligned with the top of the seaward rod and horizon. The distance a (cm) down from the top of the observer's pole where the top of the seaward pole and horizon line intersect with the observer's pole was recorded. Measurements were continued seaward by moving the landward pole 1.5 m past the seaward pole (modified from Emery 1961). This measurement of beach slope was then converted to a measure of foreshore width and standardized to a 100 cm decline in elevation from EHTL that is equivalent to the 'beach distance' measurement given by Penn and Brockmann (1994) based on their reported tidal range and is labeled Equivalent Foreshore Width (EFW).

Environmental Factors

At each sampling site and time, physical conditions were measured. These included water temperature ($^{\circ}\text{C}$), salinity, wind speed (knots) and direction, wave height (m, observed), and cloud cover (%). Proximity of observed seagrasses or other structure within sampled transects was also recorded.

Statistical analysis

Statistical comparisons of HSC CPUE and prosomal width, as well as comparisons of beach characteristics, were conducted between islands, years, and sites within island with an ANOVA or t -test as appropriate unless data failed to meet assumptions of normality or equal variance. If assumptions were not met, then an analogous non-parametric test was used. Comparisons of observed sex ratio to an expected value of 1:1 were conducted for each island with a Chi-square analysis. All statistical tests were conducted at an experimentwise type I error rate of 5%.

RESULTS

Spawning Surveys

A total of 14 spawning surveys were completed on the western end of Horn Island (2007 = 3, 2008 = 8, and 2009 = 3) and West Ship Island had 13 surveyed transects (2007 = 5, 2008 = 5, and 2009 = 3). No evidence of HSC spawning was ever found on the southern GOM side of either island, so biological data are presented for the north side only. Evidence of HSC presence in the form of exuviae was found on the north side of both islands as early as March 5th (Figure 2). The earliest live unpaired HSC were observed on the beach on 7 April 2008. The earliest date spawning activity was observed was 21 April 2008 on West Ship Island, with salinity of 13.4 and water temperature of 20.9 $^{\circ}\text{C}$. Mated pairs were not observed in 2007 until 16 May; the salinity was 27.5 on this date but had decreased from 30 on 17 April, and the temperature increased to 26.6 $^{\circ}\text{C}$ from 16.7 $^{\circ}\text{C}$. The earliest sampling date in 2009 was 23 April; the water temperature was 22.8 $^{\circ}\text{C}$, and the salinity was 18. The peak of the spawning season on both islands occurred during late April and early May in 2008. During this period, temperature increased from 17.3 $^{\circ}\text{C}$ (5 March) to 19.3 $^{\circ}\text{C}$, and salinity increased from 24.0 to 26.3. Unpaired crabs and exuviae were found through 27 September in 2007 and 13 November in 2008. The temperature was 29.9 $^{\circ}\text{C}$ and the salinity was 30.8. During the time of peak spawning activity in April/May active nesting was concentrated on the near subtidal flats rather than in the intertidal zone, likely due to the extremely narrow and steep nature of the intertidal beach.

Overall, the highest total CPUE of live animals was in 2009 (Figure 2). The CPUE was only slightly different between years on Horn Island, but was an order of magnitude higher in 2009 on West Ship compared to 2007 and 2008.

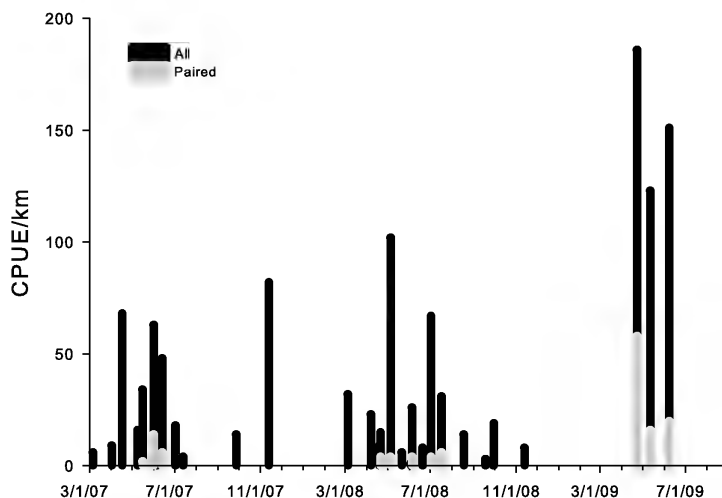


Figure 2. Horseshoe crab CPUE/km (excluding exuviae) from random beach surveys conducted within 4 hrs of the new or full moon between March 2007 and June 2009. Data for all crabs counted and those found in mating pairs are given separately. Lack of a bar outside the sampling period each year does not indicate zero CPUE.

Overall, differences in CPUE among years were significant (Kruskal–Wallis test, $p < 0.01$), but there was no significant difference in total CPUE between islands ($p > 0.05$). Spatially, all HSC spawning was observed on the north side of both islands and was most abundant on West Ship Island near Sites 10 and 18 (Figures 1d and 3) and on Horn Island near Site 5 (Figures 1e and 3).

The overall ratio of males to females was higher on the western area of Horn Island than on West Ship Island (Table 1). Both islands had proportions found to be significantly different than 1:1 based on Pearson's Chi-square test (West ship, $\chi^2_{13} = 266.737$, $p < 0.01$ and Horn, $\chi^2_{11} = 326.282$, $p < 0.001$). Mean prosomal width was not found to be significantly different between islands. The mean sizes of males and females were found to be significantly different on both West ship ($t_{(38.235)} = 13.498$, $p < 0.001$) and Horn ($t_{(59.665)} = 12.053$, $p < 0.001$) islands with an independent sample t -test, which is consistent with observed differences along the U.S. Atlantic coast and in Florida (Table 2) although mean size of both males and females were small compared to data from the middle of the species range in Delaware and the Carolinas and more similar to sex-specific mean size for the

northern edge of the range and other sites in Florida.

Physical Habitat Characteristics

Differences in substrate particle size distribution were not present among sites located at the middle/ends or with distance from shore (0 m/10 m) on Horn Island and West Ship Island (Figure 4). There were significant differences in the particle size categories -1ϕ and 3ϕ between Horn and West Ship Islands ($t_{(15)} = -2.907$, $p < 0.05$ and $t_{(17.005)} = -3.677$, $p < 0.01$, respectively) with an increase in smaller (3ϕ) particles at the 3 sites on the southern side of West Ship island (Sites WS10, WS11, WS12; Figure 1b). Overall, the north and south shores had significant differences in the 0ϕ , 1ϕ and 3ϕ particle size categories ($t_{(20.609)} = 4.450$, $p < 0.001$, $t_{(23.337)} = 5.372$, $p < 0.001$ and $t_{(11.763)} = -3.464$, $p < 0.01$, respectively).

With the exception of Site WS13 on West Ship Island, all sites had an organic content of $< 1\%$. The percent organic content was higher on West Ship Island in all categories (north and south, middle and end, 0 m and 10 m). The middle of both islands had higher percent organic content than the ends of the islands; and organic content was higher at 10 m depth than on the beach (Table 3). No clear pattern was observed for % shell hash (CaCO_3) between the

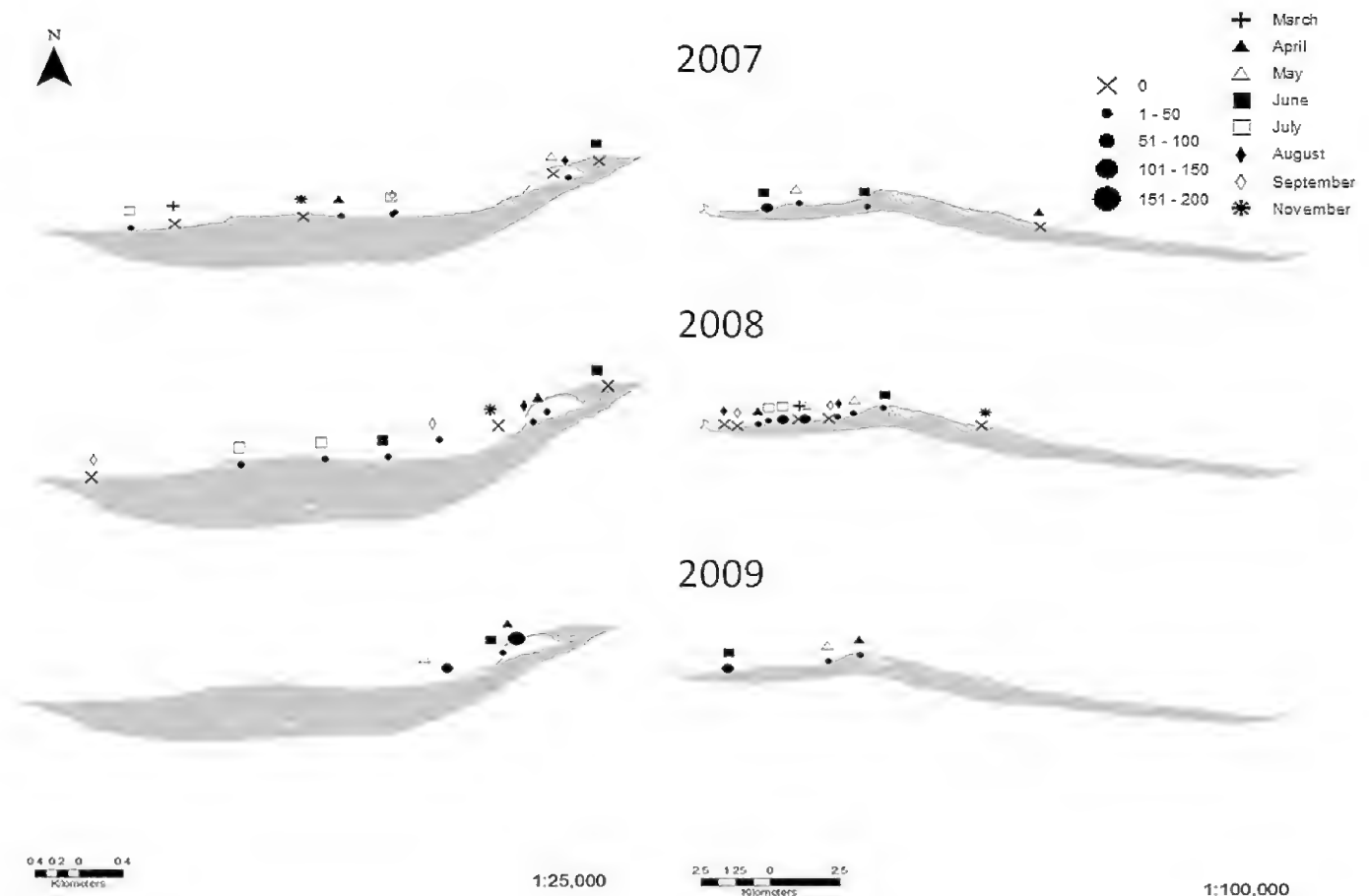


Figure 3. Spatial distribution of horseshoe crabs CPUE/km on Horn island (right) and West Ship island (left) for 2007–2009. Symbols indicating collection month within year are offset for clarity.

TABLE 1. Summary of demographic data for horseshoe crabs, *Limulus polyphemus*, observed on Horn and West Ship Islands during 2007–2009. Size metric reported is prosomal width (mm). Value in parenthesis for CPUE and size is the standard deviation.

	Horn Island	West Ship Island
Number of surveys	14	13
Mean CPUE/km	28(25)	28(23)
Female size range	149–304	152–286
Female mean size	214(36)	211(35)
Male size range	143–255	144–217
Male mean size	179(14)	179(13)
F:M ratio	1:9.76	1:5.30

islands' middle and ends or distance from shore (0 m or 10 m). However, the north shore of both islands had a greater percentage of shell hash than the south shore (Table 3). The percent organic matter and percent shell hash had no significant differences between Horn and West Ship Island, north and south sides, middle and ends, or distance from shore (0 m or 10 m).

The DRE was beyond sample maximum depth (300 mm) close to shore but decreased away from shore. All transects 70 m or less were well drained as indicated by the absence of an anaerobic layer shallower than 300 mm deep (Horn Island: 3 sites, West Ship Island: 5 sites). The transect at Site H4 on Horn Island was 80 m in total length, and a DRE was found at 50 m from shore at 111 mm depth. The DRE was found within 300 mm of the surface in all samples > 50 m from shore at this site. Sites WS7 and WS8 on West Ship Island were composed of aerobic sediment out to 90 m from shore. Sites H2 and H3 on Horn Island and Site WS9 on West Ship Island had a maximum distance from shore of 100 m. Site H3 was well-mixed throughout, whereas at Site H2 the DRE was located at 100 m from shore at 55 mm depth. The DRE was at 44 mm depth 90 m from shore and at 40 mm depth 100 m from shore at Site H9.

The length of elevation transects for both islands were standardized to a standard decline in elevation (equivalent foreshore width; EFW) from the EHTL line of 100 cm that ranged from 20–600 m on both Horn Island (Figure 5) and West Ship Island (Figure 6). Mean tidal amplitude for West ship Island in May is 0.24 m above sea level and EHTL is 0.52 m (NOAA unpublished

data) making the actual maximum foreshore width about half this distance at any given site. The shortest elevation profile is Site 18 on the east end of West Ship Island at 22.86 m. A significant difference in elevation was found between end (Sites 6–8) and middle (Sites 1–5, 9) sites on Horn Island ($t_{(10)} = -2.982$, $p < 0.05$). No other t -tests were found to be significant. On the north side of both islands, transects collected near areas of high HSC CPUE (Sites 11,12, and 18 on West Ship; Site 5 on Horn) were the longest overall at > 500 m. The elevation distance in areas of high HSC CPUE on both islands was consistently > 200 m.

DISCUSSION

Horseshoe crabs show a large degree of plasticity in spawning behavior throughout their range. This is evident in both the timing (Penn and Brockmann 1994, Sekiguchi and Shuster 2009) and the location (Badgerow and Sydlik 1989, Penn and Brockmann 1994, Brockmann 2003) of spawning activity, as well as the dominant behavioral cues (Rudloe 1985, Barlow et al. 1986, Brockmann 2003, Ehlinger et al. 2003). Typically this type of plasticity is highly localized and more pronounced at the extreme edges of a species' distribution (Fraser 1999, Haak et al. 2010), so in examining HSC spawning patterns on Mississippi barrier islands we expected to find some differences, particularly in comparison to well studied populations along the U.S. Atlantic coast and in Florida.

In some ways HSC spawning in Mississippi is predictably similar to well-studied HSC populations along the Florida Gulf coast. The spawning season in Mississippi is highly similar to HSC populations in Florida (Penn and Brockmann 1994, Ehlinger et al. 2003, Brockmann and Johnson 2011), but somewhat earlier than reported peaks in Delaware and Massachusetts (Penn and Brockmann 1994, Smith et al. 2002, Carmichael et al. 2003). This was expected as

TABLE 2. Summary of mean prosomal width (mm; \pm sd for present study only) by sex reported for horseshoe crabs, *Limulus polyphemus*, at sites along the US Atlantic coast and in Florida. Florida sites are separated by those on the Atlantic (ATL) and Gulf (GUL) coasts.

	Female	Male	Source
Maine	180	154	Moore and Perrin (2007)
New Hampshire	189	144	Watson and Chabot (2010)
Rhode Island	220	168	Shuster (1982)
Massachusetts	238	188	James–Pirri et al. (2005), James–Pirri (2010)
New Jersey	243	204	Swan (2005)
Delaware	271	210	Smith (2010)
Maryland	256	206	Swan (2005)
South Carolina	313	239	Shuster (1982)
Indian River, FL (ATL)	189	136	Ehlinger et al. (2003)
Appalchee Bay, FL (GUL)	229	171	Rudloe (1985)
Seahorse Key, FL (GUL)	227	165	Penn (1992)
Mississippi barrier island	214 (27)	179 (14)	Present study

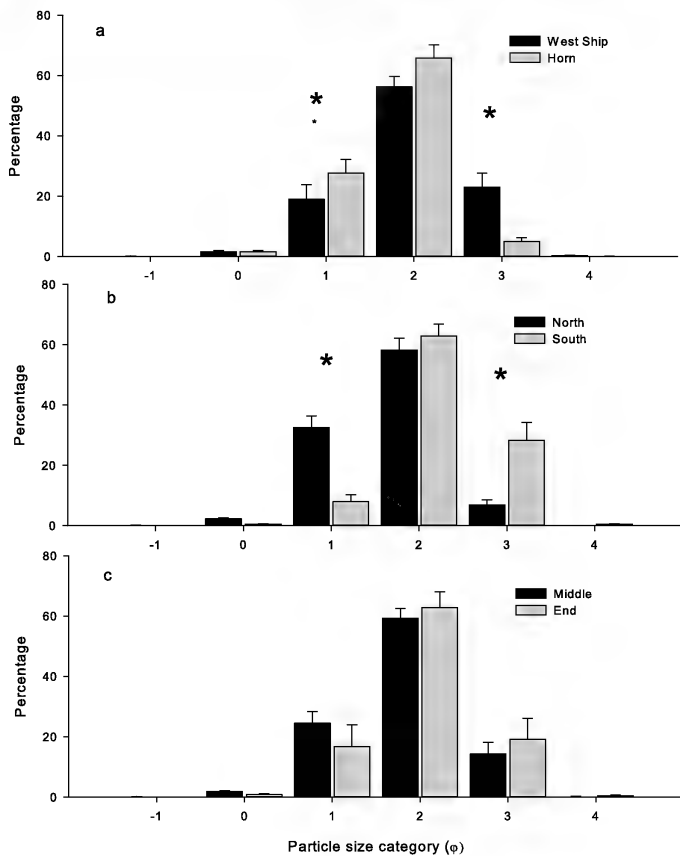


Figure 4. Particle size distribution of sediment. **a.** Comparison between islands. **b.** North and South side of islands. **c.** Middle and end of the islands. Units for grain size are $1 \phi = -\log_2(S)$ where S = particle diameter (mm). Asterisk (*) indicates a significant different between groups. Categories -1 and 4ϕ were consistently less than 0.1%.

temperature is a significant driver for the onset of spawning and nesting activity (Penn and Brockmann 1994, Jackson et al. 2008, Brockmann and Johnson 2011). Both male and female HSC in Mississippi were small in comparison to reported prosomal width in Maryland, New Jersey, and Delaware, but similar to other populations in Florida, as well as at the northern edge of their range in New Hampshire and Maine. This trend is in line with the observations of Shuster (1982) that both male and female size is highest in the middle of their range and smaller on the edges. The ratio of males to females in Mississippi was within the overall range reported for other populations along the U.S. Atlantic coast and the Florida Gulf coast, but was higher than the mean for all except for heavily harvested populations (Carmichael et al. 2003, James-Pirri et al. 2005, Mattei et al. 2010). The lower abundance of females relative to males in this population cannot be attributed to harvest, as it might be elsewhere, so the cause for this is unclear.

In terms of where HSC choose to spawn and nest, Mississippi barrier islands seem to have some unique characteristics. No spawning was

ever observed on the south side of the two islands used for this study. The only overt differences observed between the north and south side of these two islands were a higher proportion of small sediment sizes on the southern (i.e., Gulf) side, and a higher amount of wave energy. Percent shell hash across both islands was consistent with reports of percent gravel at nesting beach sites in Florida, but much lower than similar values for nesting beach sites in Delaware (Penn and Brockmann 1994). Sediment size is also related to wave energy (Malvarez et al. 2001), but typically larger particle sizes are associated with high wave action. In the case of Mississippi barrier islands this relationship was somewhat reversed and this suggests that other factors such as longshore currents or depth may affect particle size on these islands.

Based on research into *Limulus* nesting habitat conducted elsewhere, it seems that higher wave action might be the more important determinant of HSC nesting activity. Beaches with moderate wave activity in Delaware have higher HSC abundance (Smith et al. 2002) and spawning activity in a similar population near Seahorse Key along the Florida Gulf coast was concentrated on the south side where wave energy was higher (Brockmann and Johnson 2011). However, higher wave energy has been found to inhibit nesting activity and beaches in Delaware Bay sheltered from wave action by orientation or topography were identified as an important focal point for HSC conservation by Smith et al. (2011), which is consistent with our observations in Mississippi. These studies reported that wave energy probably increases the total beach area available for nesting and improves sand aeration, but that wave energy can be too high, possibly disrupting nests (Jackson et al. 2008). Quantifying total wave energy is difficult and as a result this factor is often qualitatively reported in the literature, yet wave energy can potentially be too high and probably interacts with other factors to create locally optimal conditions.

One of the more interesting observations in this study was that HSC along the Mississippi barrier islands exhibited significant amounts of sub-tidal nesting behavior. Location of spawning activity on beaches has been examined for populations in Delaware and Florida and key differences existed

TABLE 3. Summary of index elements (% organic content and % CaCO_3) of nesting beach sediment on Horn and West Ship Islands. Data summarized across sites based on location on island (end/middle; north/south) or water depth (0 m/10 m).

	% organic content					
	end	middle	north	south	0 m	10 m
Horn Island	0.17	0.21	0.21	0.22	0.17	0.27
West Ship Island	0.33	0.36	0.38	0.33	0.27	0.38
	% CaCO_3					
	end	middle	north	south	0 m	10 m
Horn Island	2.63	3.22	3.40	2.36	2.42	3.95
West Ship Island	3.02	2.44	2.27	2.05	2.77	2.17

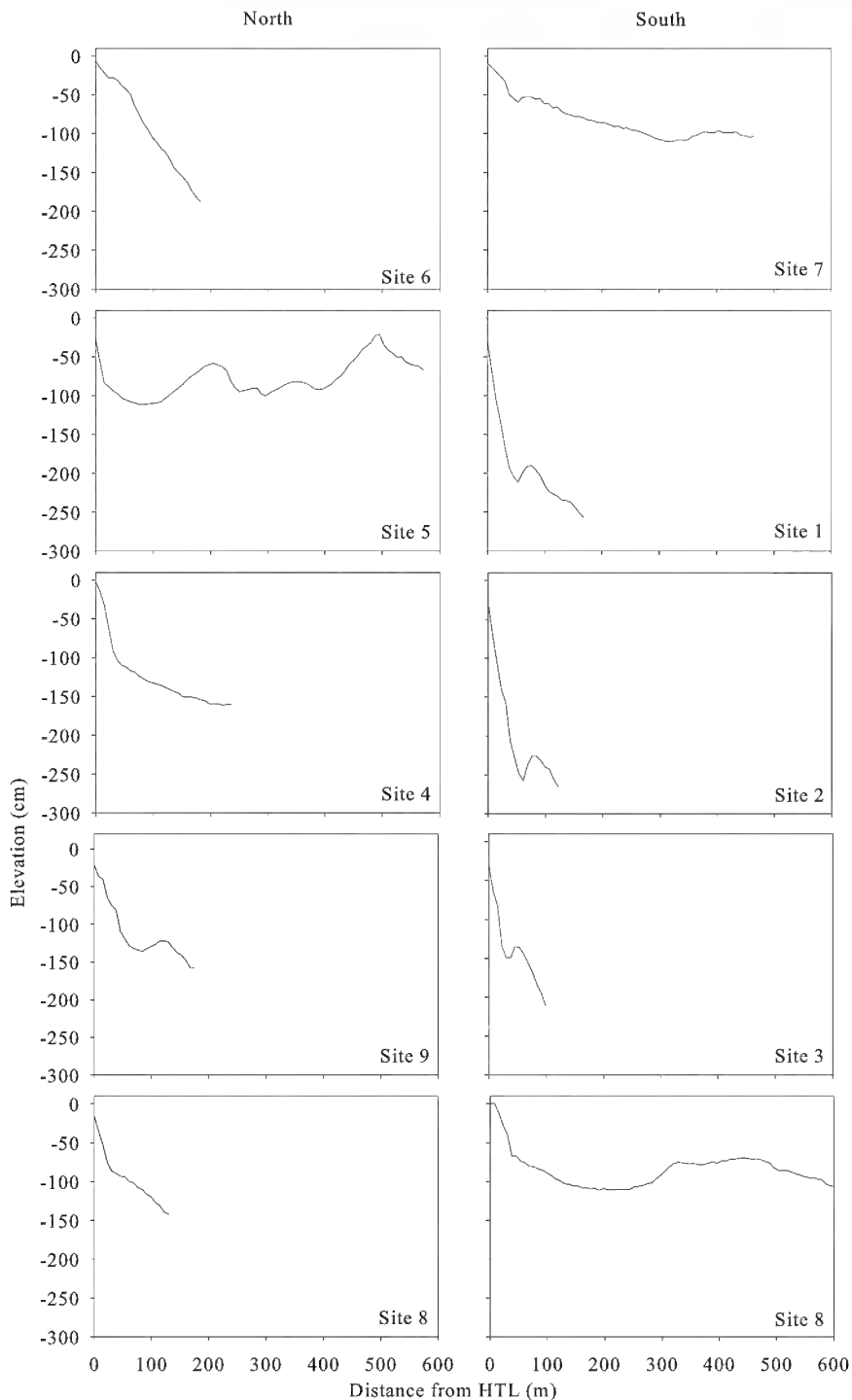


Figure 5. Elevation profiles for Horn Island from the High Tide Line (HTL). Site labels are as given in Figure 1e and are ordered with southern sites to the right and northern sites to the left with western sites at the top and eastern sites at the bottom. Sites that appear in both columns are near the end of the island; north and south samples were collected within 100 m of each other but on opposite sides of the island. See Figure 1 for details.

that were related to beach slope, beach grain size, and interstitial dissolved oxygen concentration (Penn and Brockmann 1994). Horseshoe crab nests in Delaware were found spread over a wider area including the lower beach, while nests in the Florida population were concentrated farther

from the low tide line. In addition, egg survival was found to be directly related to nest height in Florida, but not in Delaware (Penn and Brockmann 1994, Jackson et al. 2008). This was thought to be largely driven by differences in sand drainage as the smaller-sized grains on the beach in Florida were not well drained, and largely anoxic close to the low tide line, resulting in high mortality for nests in this region. In contrast, small differences in drainage were evident on the Delaware beach and nests located lower where the risk of desiccation was lower did as well as those higher on the beach. However, subtidal nesting was not reported as common on either site and it is rarely mentioned in the HSC literature although it has been reported for HSC populations in Connecticut (J. Mattei, Sacred Heart University, *pers. comm.*) and references in the grey literature suggest that sub-tidal nesting may have been observed in Florida HSC populations (A. Rudloe, *unpublished comment*).

Nesting behavior on Mississippi barrier islands was consistently observed on the sub-tidal sand flats just off the beach. These areas had a high DRE suggesting the sediment is well-oxygenated and a grain size more consistent with Delaware beaches than those in Florida (Penn and Brockmann 1994). Sub-tidal nesting behavior is not commonly reported in Delaware, but the key difference may be the lower tidal amplitude and gentle beach slope found in Mississippi. Penn and Brockmann (1994) reported a distance to a 1m decline in elevation from the extreme high tide line of approximately 12 m in Delaware, and based on their reported tidal amplitude this is a foreshore width available for inter-tidal nesting. Penn and Brockmann (1994) also reported a significant decline in egg development in the lower 2 m of the foreshore based on experimental observation that they attributed to a decline in oxygen concentration in the sediment. Similar results were reported by Jackson et al. (2008) for beaches in Delaware where egg development was significantly lower on the lower foreshore where sediment oxygen levels fell

below 3 ppm. The EFW in Mississippi was consistently over 100 m and could be as high as 500 m particularly in areas with consistent HSC presence. However the tidal range at spring tide in Mississippi is half that reported for both Florida and Delaware populations. An examination of beach pro-

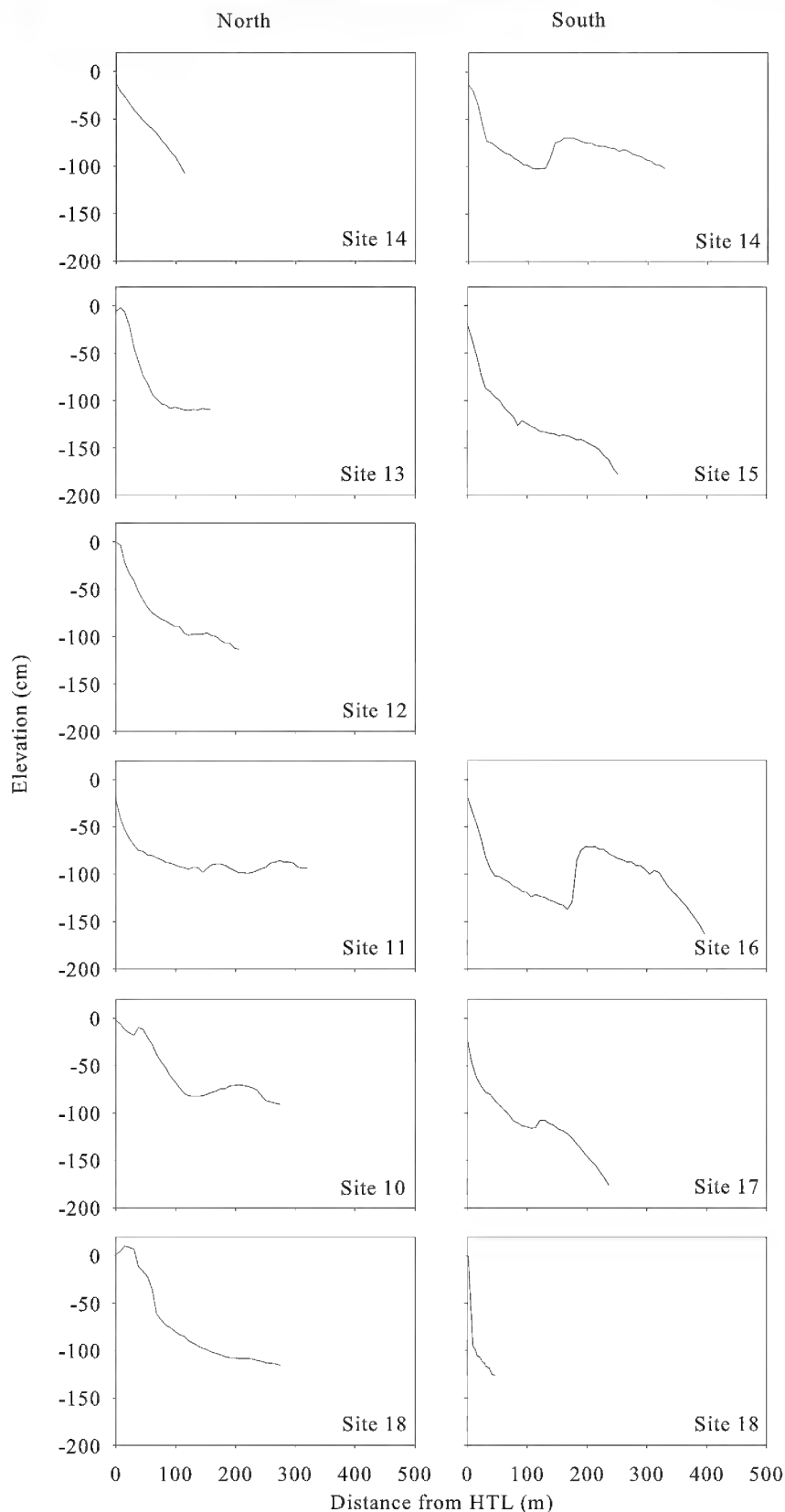


Figure 6. Elevation profiles for West Ship Island from the High Tide Line (HTL). Sites labels are as given in Figure 1d and are ordered with southern sites to the right and northern sites to the left with western sites at the top and eastern sites at the bottom. Sites that appear in both columns are near the end of the island and north and south samples were collected within 100 m of each other but on opposite sides of the island. See Figure 1 for details.

files for both islands in this study show a consistent decline from the EHTL of 0.5 m within the first 10–20 m suggesting actual foreshore width is about the same in Mississippi as in Florida and Delaware, but it is bordered on the seaward side by a much wider sub-tidal sand flat that is consistently well-oxygenated to a depth below the depth commonly reported for HSC nests (11–18 cm; Kraeuter and Fegley 1994). The well-oxygenated sediment combined with wide flat sub-tidal areas may provide unique habitat for HSC nesting in that it is not prone to desiccation, and is also well-protected from nest predation by shorebirds. Smith et al. (2002) reported that nests in Delaware were most dense within 3–5 m of EHTL and Penn and Brockmann (1994) found that nests higher on the beach showed higher percent egg development due to warmer temperatures and higher oxygen levels, so it is important to examine whether egg development and survival in subtidal nests is sufficient for them to contribute to the population. Presence of diurnal tidal cues has been provided as an important limiting factor on the range of HSC (Brockmann 2003), but evidence in Mississippi and elsewhere suggests this may not be the case (also see Ehlinger et al. 2003). Preference for intertidal nesting in HSC is generally attributed to protecting eggs and larvae from fish and invertebrate predators (Brockmann 2003). An interesting area of future study would be to examine the importance of egg and larval survivorship in areas where tidal cues for nesting are weak and well-oxygenated nest habitat is available below the low-tide line. The contribution of nesting on these islands, be it intertidal or subtidal, can only be indirectly inferred from anecdotal historical reports of HSC nesting on these islands going back over 20 years and the observed abundance of juvenile HSC in the adjacent sea grass beds in the summer (R. Heard, University of Southern Mississippi, *unpublished data*). Nonetheless, Mississippi barrier islands may represent microtidal habitat for horseshoe crab nesting similar to that reported by Ehlinger (2003) in Florida, but on a federally protected series of barrier islands which should be accounted for in management plans for the islands.

Mississippi barrier islands are subject to both natural and anthropogenic change that may alter HSC nesting habitat. Previous studies of long-term and historical characteristics of sediment transport on West Ship Island and Horn

Island indicate that these islands will continue to reduce in size (Schmid 2001). This is partially attributed to the dredged channels adjacent to the western edge of the islands that disrupt normal barrier island migration by intercepting the sediments brought by long shore transport that would build up creating elevated area on the western edge. These sediments would fill a naturally occurring or undredged area resulting in an increase in island size, as well as contribute to westward land extension and migration (Morton 2007). Barrier island restoration along the Mississippi Gulf Coast has also been a critical topic for the U.S. Army Corps of Engineers since 2005. The damage done, principally by Hurricane Katrina, fostered a study into island re-nourishment of West Ship Island and Horn Island for storm protection (USACE United

States Army Corps of Engineers, 2011). Yet, the islands are managed by the National Park Service, whose mission includes habitat protection for vulnerable populations such as nesting horseshoe crabs. From this perspective it will be vital that the characteristics of the islands, particularly the lower beach and sand flats, be maintained if they are found to be critical to local HSC nesting success (Jackson et al. 2010). More research is needed, but this study has demonstrated that HSC do commonly use Mississippi barrier island beaches for nesting, they appear to do so in a unique way that demonstrates the behavioral plasticity of this species, and these factors need to be better understood in order to properly manage the barrier island ecosystem.

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USING THE FISHES OF TEXAS PROJECT DATABASES AND RECENT COLLECTIONS TO DETECT RANGE EXPANSIONS BY FOUR FISH SPECIES ON THE LOWER COASTAL PLAIN OF TEXAS

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ABSTRACT: The Fishes of Texas project online database is a large, freely available quality controlled fish occurrence database of museum vouchered specimens. We used data from it, the same project's separate database of occurrences extracted from published literature and our own recent survey data to examine range stability for four fish species inhabiting the Texas Lower Coastal Plain: *Fundulus chrysotus*, *Fundulus jenkinsi*, *Heterandria formosa* and *Poecilia formosa*. A weakness of our data is that they consist of presences only and species absences can only rarely be inferred. To help adjust for this we used common widespread species as proxies for the four target species by using captures of these proxy species as indicators that the collecting methods used were appropriate to capture the target species, assuming then that large numbers of occurrences of the proxies with contemporaneous absence of the target species in the same samples supports inferences of probable absence of target species. We here report new and previously unpublished occurrences for these species and document westward range expansions for *H. formosa* and *F. chrysotus*, an eastward range expansion for *P. formosa*, and a pattern of possible range contraction and expansion for *F. jenkinsi*.

KEY WORDS: *Fundulus chrysotus*, *Fundulus jenkinsi*, *Heterandria formosa*, *Poecilia formosa*

INTRODUCTION

Species range expansions are often difficult to determine (West 1968, Smida and Wilson 1985, Dennis 2001). Spatially and temporally comprehensive surveys allow strong inferences regarding absences with minimal subjectivity, but typically surveys are inadequately comprehensive either spatially or temporally for use in detecting range expansions. Large datasets that cover long time periods and large geographic space are needed for this purpose. The Fishes of Texas Project database (FoTX; Hendrickson and Cohen 2011), which has been highly controlled as to quality and represents the most complete database of historical fish occurrences in Texas, is the best source for data to address range expansions and contractions for Texas' fish species. Museum data clearly and unambiguously document presence (Chapman 2005) but typically cannot rigorously address absences (West 1968). For various reasons specimens deposited in museums do not always represent the entire community present at a given location (West 1968). Susceptibility to capture varies among species, among collecting methods, and as a function of effort. Furthermore, sampling methods and effort are inconsistently reported in museum records. Additionally, collectors may deposit only selected specimens from their collections, thus creating pseudoabsences. However, the museum data are numerous, cover a large time span, and specimens can be examined for positive identification. Museum data are thus often the best data readily available for assessing changes in distributions.

We used FoTX's database of museum-vouchered species occurrences to examine potential range expansions. A "spe-

cies occurrence" is the presence of a species from a single collecting event, which is defined by a unique combination of collector(s), location and date. Species occurrences were garnered from the FoTX database of records from 40 donor institutions, coupled with the same project's database of species occurrences gathered from published literature, and our own post-2007 collections from the lower coastal plain of Texas. These are used in an attempt to detect recent spatial changes in fish distributions. Our recent collections are all backed by museum voucher specimens and are otherwise typical of museum specimen-based occurrence data in that they come from collecting events conducted irregularly over space and time using non-standardized methods and effort. Our preliminary analyses of these combined data sets identified *Fundulus jenkinsi*, *F. chrysotus* (Fundulidae), *Heterandria formosa* and *Poecilia formosa* (Poeciliidae) as likely to have experienced range expansions within the time-frame of our data and we report on our detailed explorations of that hypothesis for these target species. We are aware of other freshwater native species with apparently expanding ranges along the coast (e.g., *Herichthys cyanoguttatum* and *Astyanax mexicanus*), as well as non-natives (e.g., *Lucania goodei*, *Oreochromis aureus*, *Ctenopharyngodon idella*, *Pterygoplichthys* sp.) but we do not address those here.

MATERIALS AND METHODS

Our study area (Figure 1) includes the following ecoregions described by Griffith et al. (2004): Texas-Louisiana Coastal Marshes, Northern Humid Gulf Coastal Prairies, Southern Humid Gulf Coastal Prairies, Flatwoods, Coastal

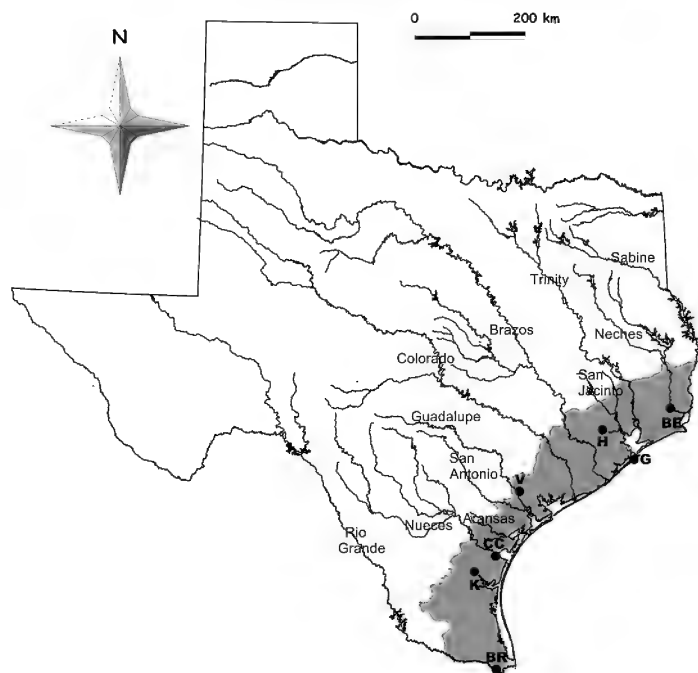


Figure 1. Texas Lower Coastal Plain (TLCP) with geographic features (river drainages) to aid in orientation. The TLCP is indicated by gray. TLCP cities: BE = Beaumont; BR = Brownsville; CC = Corpus Christi; G = Galveston; H = Houston; K = Kingsville; V = Victoria.

Sand Plain, Lower Rio Grande Valley, Lower Rio Grande Alluvial Floodplains, and Floodplains and Low Terraces associated with each of these ecoregions. We refer to this area as the Texas Lower Coastal Plain (TLCP).

Species absences cannot typically be inferred from museum–vouchered occurrence data but we here explore a way to ameliorate that inherent bias to at least some degree. We chose to analyze presences of target species against a collection background defined by the occurrences of a proxy species. Proxy species are those species that, if collected, constitute evidence that collection methods were likely not biased against collection of the target species and can be used to approximate absences of a target species when the proxy species is collected and the target species is not. While this logic is not necessarily always appropriate, we believe it is effective in this application where many collection locations are included in the analysis. Proxy species were chosen based on: 1) they must be generally as easily collected as the target species (i.e., they would be similar to the target species in size and general body shape and occur in the same microhabitats); and 2) they must be more commonly collected and wider–spread than the target species, but where ranges overlap, known to frequently co–occur with the target species.

To analyze ranges of our target species *H. formosa*, *F. chrysotus* and *F. jenkinsi*, we use *Gambusia affinis* as proxy, and for *Poecilia formosa* we use *P. latipinna* as proxy. We queried for species occurrence records (a “species occurrence” is the presence of a single species from a single collecting event) of

the target and proxy species on the TLCP in the FoTX’s database of 124,390 museum–vouchered species, together with the project’s database of 12,037 species occurrence records gathered from published literature (FoTX Literature and Other Unvouchered Database; <https://sites.google.com/site/fishesoftexasdocumentation/future-directions/addition-of-literature-and-other-non-vouchered-sources>) as well as our recent collection records not yet in the FoTX database. Species occurrence records having georeferencing errors greater than 10 km were discarded prior to analysis. Because the boundaries between the study area and the adjacent ecoregions are not precise and because there is an error associated in georeferencing the capture locations (Hendrickson and Cohen, 2011), specimens from neighboring ecoregions captured within 5 km of the border of our study area are included in our analyses. As part of the FoTX project, many specimens had been previously examined for accurate identifications but we also identified an additional 312 lots of *P. latipinna* cataloged at University of Texas at Austin’s Texas Natural History Collection (TNHC) from unopened jars in an effort to find misidentifications of *P. formosa* and other coastal species.

In addition to these data sets available currently from the FoTX project, we included our own recent survey data in our analysis. Over 4 years (2008 – 2011) we sampled at 60 locations on the TLCP. Inspection of the FoTX database indicated that most of these locations were either previously unsampled or had not been sampled in 20 or more years. We generally used a 3 m seine with 4.8 mm delta mesh and/or a 1 m x 1 m frame net with 3.2 mm delta mesh. At 5 locations we exclusively sampled with a 3.2 mm delta mesh dip net. Sites were sampled until all available major habitat types had been sampled or for 5 seine hauls after the last new species for the site was collected. Vouchers of all species from each site were deposited in the TNHC and will eventually be added to the FoTX database.

For analysis we combined all 3 data sets. Less than a quarter of the total collecting events occurred in the first 100 years (1850 to 1949) and more than three–quarters were in the last 60 years. The collection effort was examined by era: 1850 to 1949 (738 total collecting events), 1950 to 1969 (997), 1970 to 1989 (1392) and 1990 to 2010 (539). However, because there are no known records of *H. formosa* in Texas before the 1980s, for that species the temporal data set was divided into only two eras; “before 1980” (2570 total collecting events) and “after 1980” (1160 collecting events). Maps of all collections of target species and their proxies were produced for each species and era and are the basis of our analysis.

RESULTS AND DISCUSSION

Our query of the FoTX museum vouchered database produced 1,351 occurrence records, 295 of which had been pre-

viously verified by the FoTX project staff (via examination of preserved specimens). These newly verified records included 15 records cataloged as *F. jenkinsi*, 5 records cataloged as *F. chrysotus*, 33 records cataloged as *P. latipinna*, and a single record of *H. formosa*. The later record, from the Sabine River collected in 1986, represents the first documented occurrence of this species in Texas. In our estimation, no records of *P. formosa* from this database required verification. Only one of the TNHC's 312 lots of *P. latipinna* examined contained any misidentified specimens. The same query of the FoTX literature database added 216 records and our recent surveys added 111 more occurrence records. All records were

TABLE 1. Numbers of data records used in analysis from the Fishes of Texas (FoTX) vouchered data (V), FoTX literature data (L) and our recent collections.

Date Range	FoTX (V) 1891— 2004	FoTX (L) 1950— 2011	Recent 2008— 2011	TOTAL 1891— 2011
No. of Locations	679	143	60	882
No. of Species				
Occurrence Records	1351	216	111	1678
<i>H. formosa</i>				
Occurrence Records	3	0	6	9
<i>F. jenkinsi</i>				
Occurrence Records	16	7	2	25
<i>F. chrysotus</i>				
Occurrence Records	78	6	21	105

combined (Table 1) and used in the analysis.

Collecting effort and geographic distribution varied over time (Figure 2). The collecting events prior to the 1950s were concentrated in the areas around the Galveston–Trinity Bay complex tributaries, Corpus Christi and the bays and streams immediately east and northeastward, and the lower Rio Grande valley with its associated resacas and irrigation ditches. Over the same time period the area between the Aransas River (about 35 km east of Corpus Christi) and the Galveston Bay drainages experienced comparatively much less collecting effort. The same area appears still to be slightly less intensively sampled during the most recent sixty years of sampling effort, thus compromising to some degree our ability to make inferences regarding distributions over time. Note that there are records of sampling events on the TLCP as early as 1851 but neither our target species nor the proxy species have collection records prior to 1891 despite 88 collection events for the time period.

It is helpful to examine occurrence records in the context of a background of known absences. One could easily define a range on a map of presence and absence points, but since we lack true absences we also examine plots of proxy species occurrences that we posit represent probable target species absences. Use of *P. latipinna* as a proxy for *P. formosa* is partic-

ularly appropriate since *P. formosa* is gynogenetic and dependent on males of *P. latipinna* to activate its eggs; thus its distribution is entirely restricted to locations where *P. latipinna* occurs. Use of *G. affinis* as a proxy for our other target species is appropriate because it meets the requirements specified above. Use of *G. affinis* (usually freshwater) as a proxy species for *F. jenkinsi* (usually brackish water) is supported both by similarity in size and by general habitat preferences. It has been observed that *G. affinis* is better adapted physiologically to brackish marshes than it is to freshwater (Martin et al. 2009), as is *F. jenkinsi*. Simpson and Gunter (1956) reported *G. affinis* and *F. jenkinsi* from nearly the same salinity range in Texas marshes and streams as did Peterson and Ross (1991) for Mississippi locations. Furthermore, in Texas all known locations for *F. jenkinsi* are also locations where *G. affinis* has been collected, not necessarily at the same collecting event. This method does not eliminate all subjectivity but we believe it the best available method for detecting range changes over time.

Fundulus chrysotus (Figure 3) — This species had not been reported west of Houston, TX prior to 1973, but in 1973 it was reported about 8 km west of Houston and from the Guadalupe River near Victoria, TX, about 200 km southwest of Houston. By 1979 it was reported from the Aransas National Wildlife Refuge (ANWR), about 240 km southwest of Houston. Recently *F. chrysotus* has been found to be locally abundant at sites adjacent to the ANWR (H.D. Hoese, pers. comm., University of Louisiana at Lafayette, Lafayette, LA, retired), but our collections from further west failed to include it indicating perhaps that the western edge of the range may currently be more or less stabilized.

Whiteside and Berkhouse (1992) reported this species from the Guadalupe River drainage based on collections from 1991. They referred to this as an eastern Texas species and appear to have been unaware that it had been collected in 1973 from the Guadalupe River near Victoria, TX and in 1979 further west on the ANWR. While our data cannot rule out introduction at their Guadalupe location, which was further inland and off the lower coastal plain, our data indicate that this species was well-established in the drainage basin before their report. Lack of collections of *F. chrysotus* despite a strong collecting effort in the Guadalupe drainage from 1950–1969, indicated by more than 40 captures of this species' proxy, *G. affinis* (Figure 3B), support our conclusion that the species most likely expanded into the Guadalupe drainage sometime between 1950 and 1973. The expansion appears to be a physical range expansion since the species has now been reported from the Guadalupe River basin 5 times between 1973 and 2011, a sure indication of a reproducing population.

Fundulus jenkinsi (Figure 4) — Except for one specimen collected near the Sabine River in 1953, all pre-1969 Texas records of *F. jenkinsi* were from the Galveston–Trinity Bay

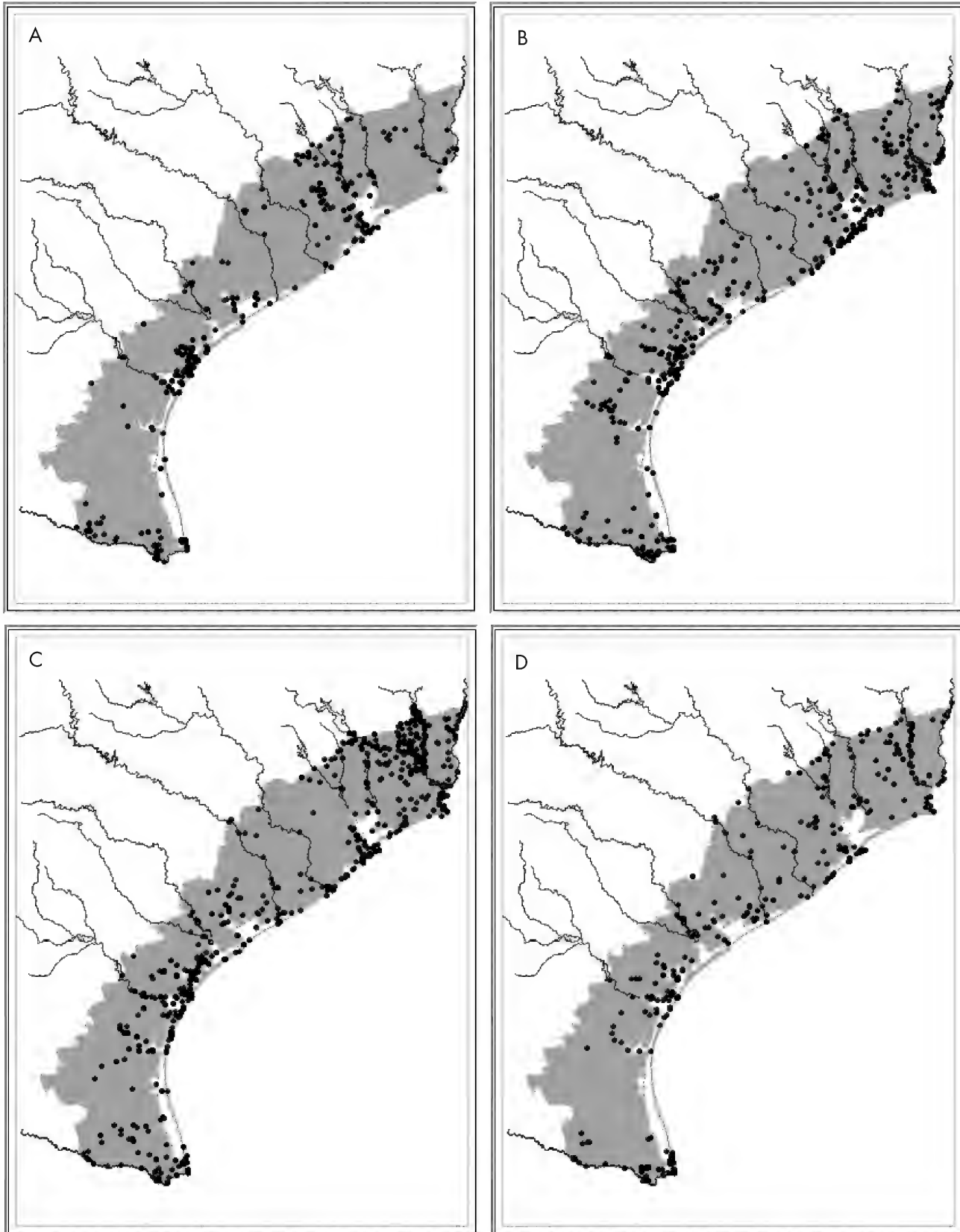


Figure 2. Numbers of collecting events through time and their distribution. Total number of collecting events was 3666. **A.** Distribution of collecting events, 1851 – 1949, 738 collecting events; **B.** Distribution of collecting events, 1950 – 1969, 997 collecting events; **C.** Distribution of collecting events, 1970 – 1989, 1342 collecting event; and **D.** Distribution of collecting events, 1999 – 2010, 538 collecting events.

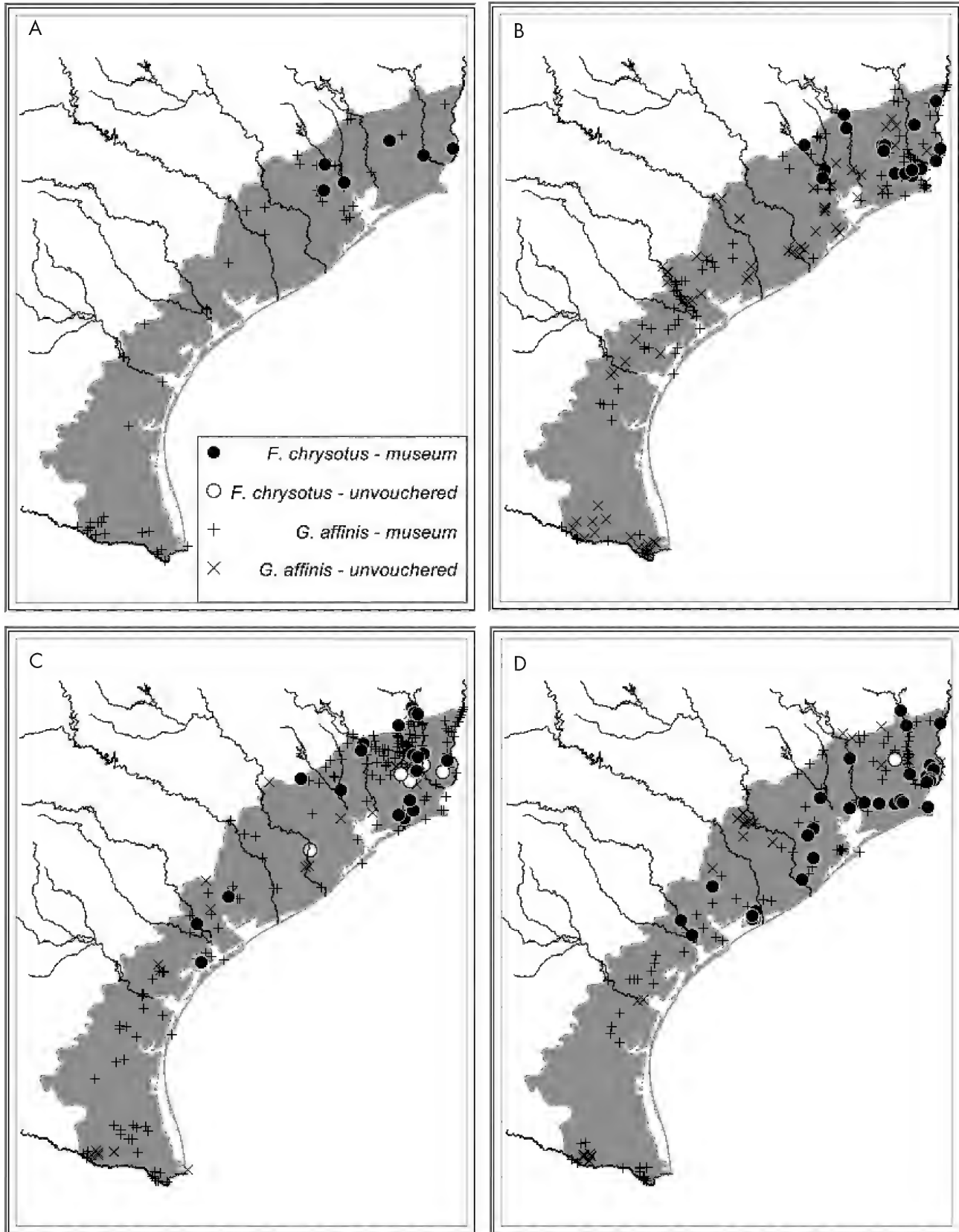


Figure 3. Distribution of *Fundulus chrysotus* and its proxy, *Gambusia affinis* through time. The total number of occurrence records for this species is 105 compared to 718 occurrences for *G. affinis* within the total geographic range occupied by *F. chrysotus* through the entire period. **A.** 1851 – 1949. *F. chrysotus* – 7 occurrence records; *G. affinis* – 13 occurrence records within the *F. chrysotus* range for the time period and 27 within the total *F. chrysotus* range; **B.** 1950 – 1969. *F. chrysotus* – 19 occurrence records; *G. affinis* – 98 occurrence records within the *F. chrysotus* range for the time period and 147 within the total *F. chrysotus* range; **C.** 1970 – 1989. *F. chrysotus* – 40 occurrence records; *G. affinis* – 395 occurrence records within the *F. chrysotus* range for the time period and 395 within the total *F. chrysotus* range; **D.** 1999 – 2010. *F. chrysotus* – 39 occurrence records; *G. affinis* – 149 occurrence records within the *F. chrysotus* range for the time period and 149 within the total *F. chrysotus* range.

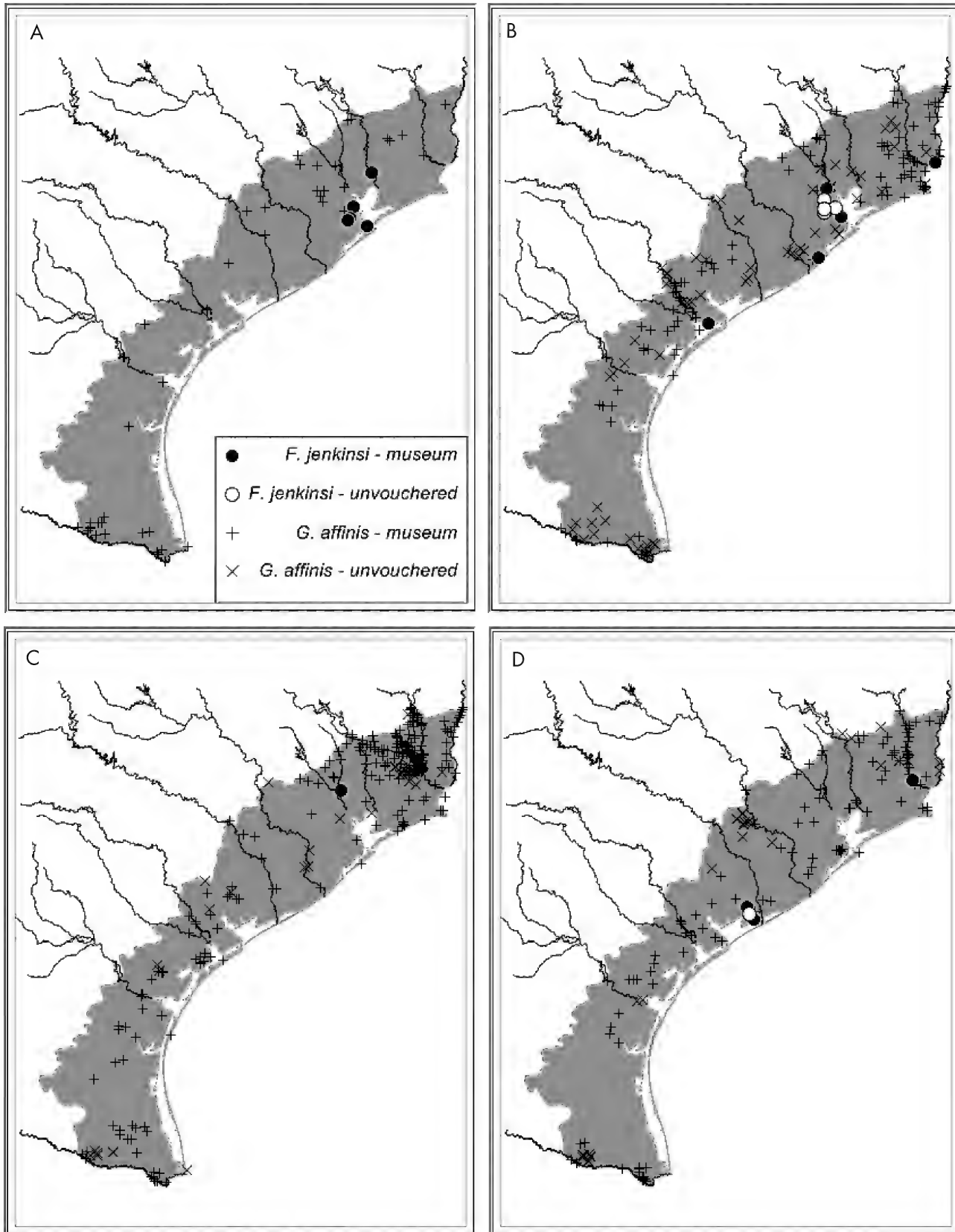


Figure 4. Distribution of *Fundulus jenkinsi* and its proxy, *Gambusia affinis* through time. The total number of occurrence records for this species is 25 compared to 239 occurrences for *G. affinis* within the total geographic range occupied by *F. jenkinsi* through the entire period. **A.** 1851 – 1949. *F. jenkinsi* – 5 occurrence records; *G. affinis* – 6 occurrence records within the *F. jenkinsi* range for the time period and 20 within the total *F. jenkinsi* range; **B.** 1950 – 1969. *F. jenkinsi* – 11 occurrence records; *G. affinis* – 83 occurrence records within the *F. jenkinsi* range for the time period and 83 within the total *F. jenkinsi* range; **C.** 1970 – 1989. *F. jenkinsi* – 1 occurrence record; *G. affinis* – 65 occurrence records within the *F. jenkinsi* range for the time period and 65 within the total *F. jenkinsi* range; **D.** 1999 – 2010. *F. jenkinsi* – 8 occurrence records; *G. affinis* – 71 occurrence records within the *F. jenkinsi* range for the time period and 71 within the total *F. jenkinsi* range.

complex. In 1969 the species was taken about 50 km WSW of Galveston in Salt Lake, Brazoria County, TX, and 24 km SE of Green Lake, Calhoun County, TX, about 190 km SW from Galveston. Since then it appears that the westernmost record of *F. jenkinsi* was in 2010 in the Tres Palacios River about 135 km SW of Galveston. From 1970 to 1989 there was only one report (in 1981 from the San Jacinto drainage) of *F. jenkinsi* from the whole of the TLCP despite 83 records of *G. affinis* (Figure 4C) within the range of *F. jenkinsi*. There are no reports of this species from the Galveston–Trinity Bay complex since 1951 despite 231 records of *G. affinis* within the overall range of *F. jenkinsi*.

Fundulus jenkinsi is generally considered sporadic in distribution and rare where found; however, Peterson et al. (2003) found it much more abundant than expected in eastern Mississippi and western Alabama coastal areas. Rozas (1992) and Rozas and Reed (1993) reported it rare in a Louisiana marsh; however, when Peterson and Turner (1994) sampled the same marsh less than 9 months earlier using a different sampling method (flume nets), they found it to be the ninth most abundant species captured. Recently, Lopez et al. (2011) found *F. jenkinsi* from Louisiana through the panhandle of Florida to be patchy but more abundant when salinity was <16. We collected it in 2010 in the Tres Palacios River in Texas, a new freshwater location for the species, and found it locally abundant. However, our recent collections in the Galveston–Trinity Bay drainages, where it was historically collected, failed to include it. Thus, our data support a hypothesis that populations of this species may fluctuate dramatically.

Extensive human development in the Galveston–Trinity Bay drainages may explain why there have been no collections reported for this species in this area for 30 years. Because proxy data show that since the most recent record of *F. jenkinsi* there has been a large amount of sampling (30 occurrences of *G. affinis*) in Galveston–Trinity Bay drainages that would likely have detected *F. jenkinsi*, this species may have been extirpated from these drainages. We sampled only lightly in this area and believe that more sampling is necessary to rule out its presence. Existing museum collections should also be re-examined since our limited examination of some of them found this species often confused with *G. affinis*, *F. chrysotus* and *Fundulus pulvereus*. It is possible that populations of this species persist in the Galveston–Trinity Bay drainages, and that lack of evidence of persistence could be attributable to misidentifications.

Poecilia formosa (Figure 5) – The first records of *P. formosa* from the TLCP are from the Rio Grande drainage in 1923 in spite of 16 collecting events prior to 1923 in this drainage. The earliest records for *P. formosa* outside the Rio Grande valley are from the Nueces River and include a museum–vouchered 1952 collection from the Nueces River, a published record from 1964 (Martin 1964), and an unvouchered

collection of 199 individuals (Menn 1965). Specimens from Petronila Creek (1965) and San Fernando Creek (1966), both near the Nueces River but not in its drainage, suggest that the species was widely distributed in the area between Kingsville and the Nueces River in the 1960s. A 1975 collection from the Rob and Bessie Welder Wildlife Foundation Refuge in the Aransas River drainage extended the perceived range eastward by a little more than 35 km. More eastern records were unknown until we collected this species in 2008 in the Brazos River near Rosharon, TX, an expansion in perceived range of a bit more than 200 km. The proxy species, *P. latipinna*, was reported between the Aransas and Brazos rivers in 60 collections from 1970 through 2010, indicating that the species was likely not present in this area until recently.

Darnell and Abramoff (1968) indicate that one reason why there is so much confusion regarding the native range of this species in Texas is because until 1932, when C.L. Hubbs clarified the systematics of this species, all Texas specimens were attributed to *Poecilia sphenops*. Darnell and Abramoff consider populations in the few minor drainages of the Laguna Madre in Texas and in the lower Nueces River to be native. They used presence of *P. formosa* in the creeks around Kingsville to suggest that Martin (1964) was probably wrong in his speculation that *P. formosa* had been introduced into the lower Nueces between 1953 and 1960. The historic record includes only two pre–1953 records of *P. latipinna* from the Nueces so it is likely that the species was in fact present in the Nueces, but not detected due to limited sampling. A hypothesis that *P. formosa* is native to the Nueces is not ruled out by our data.

Heterandria formosa (Figure 6) – This species was first collected from Texas in 1986 and again in 1987 from the Sabine River at the I–35 bridge. In 2003 it was again documented in the Sabine River in Jefferson County, TX. Our 2010 targeted efforts to collect *H. formosa* consisted of 2 days collecting that resulted in 6 new locations for the species as far west as Ogden Ditch in Chambers County, TX between the Neches and Trinity basins.

This small species, with females sometimes reaching a maximum of only 30 mm SL (Boschung and Mayden 2004), can be easily missed using standard collecting methods. However in Texas, collectors have sampled extensively and often using appropriate gear (as estimated by the 158 occurrence records of its proxy species, *G. affinis*, within the current known range of *H. formosa*) for many years prior to its first collection and failed to find it. The first specimens were collected by Hanks and McCoid (1988) who state that bi-annual sampling at the Sabine River site for 10 years before 1986 provided strong circumstantial evidence that it was previously absent at that site. In addition, they cite 10 years of collection by other personnel on the Texas side of the Sabine with no reports of *H. formosa*, further supporting their contention that this population was the result of

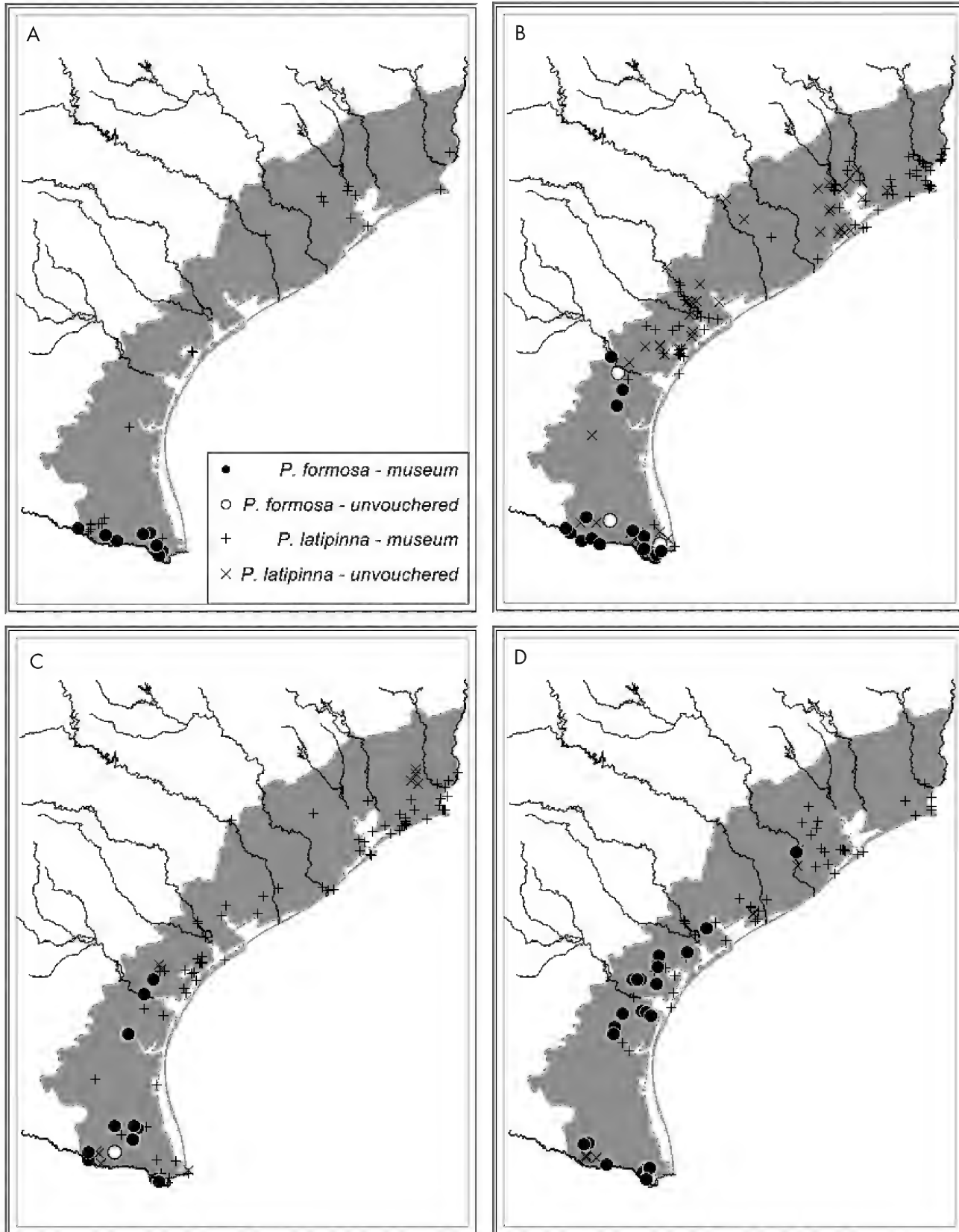


Figure 5. Distribution of *Poecilia formosa* and its proxy, *P. latipinna* through time. The total number of occurrence records for this species is 131 compared to 332 occurrences for *P. latipinna* within the total geographic range occupied by *P. formosa* through the entire period. **A.** 1851 – 1949. *P. formosa* – 13 occurrence records; *P. latipinna* – 24 occurrence records within the *P. formosa* range for the time period and 29 within the total *P. formosa* range; **B.** 1950 – 1969. *P. formosa* – 36 occurrence records; *P. latipinna* – 67 occurrence records within the *P. formosa* range for the time period and 126 within the total *P. formosa* range; **C.** 1970 – 1989. *P. formosa* – 23 occurrence records; *P. latipinna* – 31 occurrence records within the *P. formosa* range for the time period and 70 within the total *P. formosa* range; **D.** 1999 – 2010. *P. formosa* – 59 occurrence records; *P. latipinna* – 107 occurrence records within the *P. formosa* range for the time period and 107 within the total *P. formosa* range.

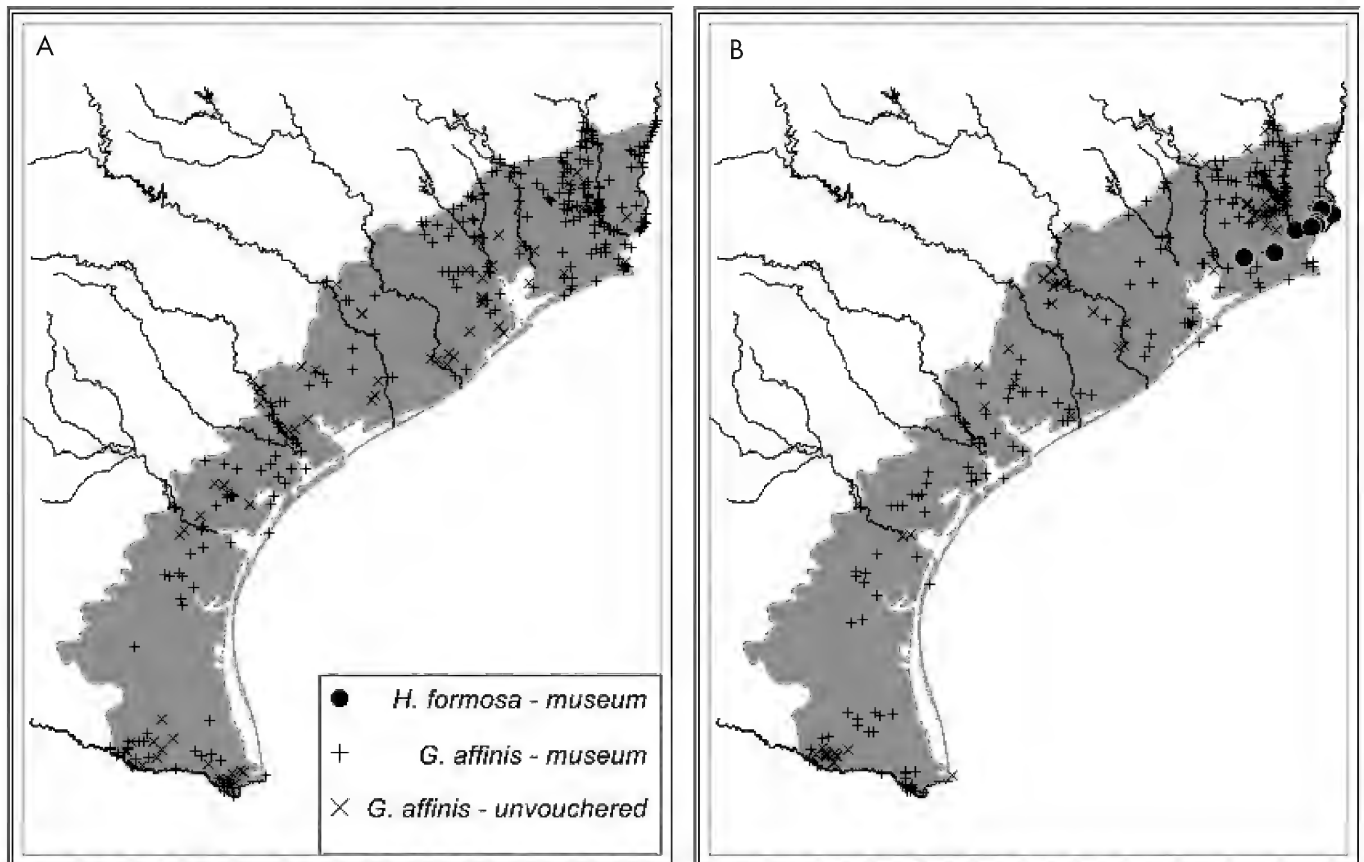


Figure 6. Distribution of *Heterandria formosa* and its proxy, *Gambusia affinis* through time. The total number of occurrence records for this species is 13 compared to 158 occurrences for *G. affinis* within the total geographic range occupied by *H. formosa* through the entire period. **A.** 1851 – 1979. *H. formosa* – 0 occurrence records; *G. affinis* – 0 occurrence records within the *H. formosa* range for the time period and 103 within the total *H. formosa* range; **B.** 1980 – 2010. *H. formosa* – 13 occurrence records; *G. affinis* – 55 occurrence records within the *H. formosa* range for the time period and 55 within the total *H. formosa* range.

a recent colonization event. Also supporting the hypothesis that the Texas populations are the results of recent colonization rather than early sampling bias that failed to document them, D.L. Bechler (pers. comm., Valdosta State University, Valdosta, GA) collected extensively in southeastern TX from 1982–1995 and failed to find *H. formosa* in any locations other than that reported by Hanks and McCoid.

Chaney and Bechler (2006) speculate that *H. formosa* is often missed in collections because standard collecting seines usually have mesh sizes that *H. formosa* can pass through. While this may be true, we have collected the species (especially large gravid females) in Texas with mesh sizes as large as 4.8 mm (delta mesh). This species occurs in dense vegetation which tends to clog nets and reduce the effective mesh size. While inappropriate gear may explain overlooking some individuals, this alone cannot explain the total absence of *H. formosa* in the many collections (163 collection records for *G. affinis* from within the current range of *H. formosa*) prior to 1986.

Because of the preference for backwaters which are often ephemeral and which frequently dry, this species may be especially good at both colonization and recolonization (Baer

1998). Chaney and Bechler (2006) consider the flatwoods ecoregion of Georgia to be the most utilized ecoregion for *H. formosa* in that state. If this is true in Texas, we would predict that this species will soon expand its range up the Neches and Sabine Rivers further into the Texas Flatwoods ecoregion.

SUMMARY

The distribution patterns over time seen for these 4 species are consistent with there being no direct intentional movement by humans. However, we can only speculate as to what events and factors have allowed these changes in distribution. Climate change may be one factor aiding range extension or contraction via creation of preferred environmental conditions in uncolonized areas and degradation of historic habitats, but for all of our target species the causes for range expansions are unknown and difficult to determine. We believe they are probably natural events rather than the result of human introductions. All of our target species are fairly tolerant of high salinities and can cross basins by travelling along the coast, especially during times of relatively low salinity. Inland fish populations are highly restricted to their ba-

sin of origin and not able to cross basin divides, despite what may be favorable conditions in neighboring basins. However, along the coast these divides are not well defined and individuals can move between basins during high water events that connect basins or freshen bays, thus creating freshwater connections between basins. Human modifications of drainage basins through flood control channelization, ditching for drainage of farm land, and building canals for irrigation water transfer and commercial transportation certainly contribute as well. Bait bucket releases cannot be ruled out, but are not likely for these species (except perhaps *P. formosa*,

which is occasionally used as bait).

The data this study is based upon are less complete than we might hope, and we find, for example, relatively large spatial and temporal gaps in coverage, especially along the Texas coast between the Guadalupe and Brazos River basins. More historical data are needed to obtain a complete picture. Published scientific articles, dissertations, theses and government reports represent a large source of historic occurrence data but extracting and entering those occurrences into a data base is a large task, which the FoTX is beginning to do.

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SHORT COMMUNICATION

EVIDENCE OF SPAWNING CAPABLE TARPON (*MEGALOPS ATLANTICUS*) OFF THE LOUISIANA COAST

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KEY WORDS: *Megalops atlanticus*, Northern Gulf of Mexico, Spawning

INTRODUCTION

Despite the fact that the tarpon (*Megalops atlanticus*) is a popular sport fish in the Gulf of Mexico (GOM; Ault et al. 2008), little is known of its spawning behavior. Spawning *M. atlanticus* have never been documented and fertilized eggs have not been observed *in situ* (Ault et al. 2008). While it has been suggested that adult *M. atlanticus* move to deep water off the southwest coast of Florida and into the Yucatan Channel to spawn, the actual locations of spawning grounds remain unknown (Smith 1980, Crabtree et al. 1995, Crabtree et al. 1997). Distribution patterns of larvae (leptocephali) have served as the basis for most of what has been inferred about the spawning areas (Smith 1980, Crabtree et al. 1997). For example, leptocephali were collected from the southwestern GOM, the Yucatan Channel, and along the west coast of Florida, and based on their size, it was assumed that *M. atlanticus* spawned in nearby areas (Smith 1980).

Histological examination of gonads has also been used to estimate the location of *M. atlanticus* spawning habitat. Females collected from the Florida Keys and Boca Grande Pass off the west coast of Florida and contained ovaries with post ovulatory follicles (POF) and advanced vitellogenic oocytes, suggesting *M. atlanticus* spawn in this region from April through July (Crabtree et al. 1997). Examination of gonads from *M. atlanticus* caught off the coast of equatorial Ceara State, Brazil suggested that spawning occurs there from October through January (de Menezes and Paiva 1966). We report here the first evidence of spawning capable *M. atlanticus* off the coast of Louisiana in the northern GOM based on histological examination of gonads.

MATERIALS AND METHODS

Two large, sexually mature *M. atlanticus* (one female, one male) were collected by anglers about 30 km south of Venice, Louisiana on 2 July 2011. A second male was captured by anglers on 28 July 2011 from the same area. Fish were weighed (kg) and measured (mm fork length, FL) and gonadal tissue from each specimen was removed, weighed, and

fixed whole in 10% neutral buffered formalin within 12 h of capture. Gonadal tissue was processed following standard histological techniques, embedded in paraffin, sectioned at 4 µm and stained with hematoxylin and eosin. Reproductive phases and gamete stages were determined following Brown-Peterson et al. (2011).

RESULTS AND DISCUSSION

The female *M. atlanticus* weighed 56.8 kg and was 1778 mm FL. The first male weighed 55.5 kg and was 1676 mm FL; the second male weighed 56.6 kg and was 1698 mm FL. These fish were within the same size ranges as reported for spawning *M. atlanticus* from Brazil and Florida (de Menezes and Paiva 1966, Crabtree et al. 1997).

The female was classified as spawning capable based on the presence of both late vitellogenic oocytes and 24 h POF in the ovaries at the time of collection (Figure 1A). The warm water at the time of specimen collection in combination with less than optimal fixation resulted in rapid degradation of the POF observed. However, these POFs appear similar to 24 h POF from other species collected at similar water temperatures (Brown-Peterson et al. 2011) and provide evidence that this female spawned 24 h or less prior to capture. While the ovary was dominated by tertiary vitellogenic oocytes (Vtg3), there was evidence of asynchronous oocyte development because secondary vitellogenic (Vtg2) were also present (Figure 1A). The two males were also both classified as spawning capable. Testes were full of spermatozoa but there was no active spermatogenesis occurring (Figure 1B), suggesting the males were at the end of the reproductive season but still capable of releasing spermatozoa. These specimens were collected near the end of the reported spawning season for *M. atlanticus* in Florida (Crabtree et al. 1997).

The collection of both male and female *M. atlanticus* in the spawning capable phase suggests that *M. atlanticus* may be spawning off Louisiana and represents the first evidence that this species appears to be reproducing in the northern

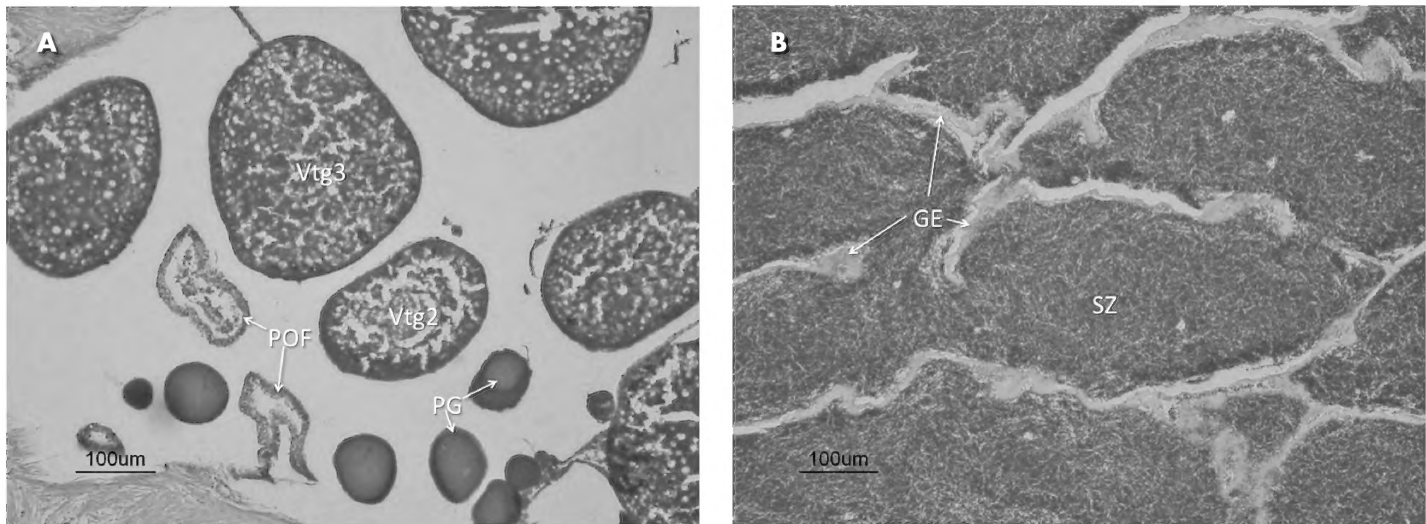


Figure 1. Histological images of gonadal tissue in the spawning capable phase from *M. atlanticus* collected off the coast of Louisiana on 2 July 2011. **A.** Female. **B.** Male. Key: PG—primary growth oocyte; POF—24 h postovulatory follicle; Vtg2—secondary vitellogenic oocyte; Vtg3—tertiary vitellogenic oocyte; GE—germinal epithelium; SZ—spermatozoa.

GOM. Juvenile *M. atlanticus* have been reported from Mississippi coastal locations by Franks (1970), Overstreet (1974) and Schofield et al. (2007). Various suggestions have been made to account for the presence of juvenile *M. atlanticus* on the coasts of Louisiana¹ and Mississippi² (Franks 1970, Overstreet 1974,

Schofield et al. 2007). It is possible that these juveniles are the product of local spawning activity based on evidence provided here. Additional collections of adult *M. atlanticus* during the spring and summer from the northern GOM would help elucidate reproductive activity of this species.

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